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SYMPOSIUM ISSUE
PROBLEM-BASED LEARNING

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Cover Photographs

Acheta domesticus **(L.)**, the European house cricket, a popular organism for physiological and developmental studies as well as for fishing. From 1:00 counterclockwise are shown females as last instar nymph, ecdysiate from molt to the adult form, untanned adult immediately after ecdysis, and young tanned adult.

Photo Credit Jim Bradley

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AUTHENTIC ASSESSMENT OF PROBLEM-BASED LEARNING

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ABSTRACT

In the quest to nurture the whole student, nursing faculty have sought more engaging strategies of teaching and learning. One of these strategies is problem-based learning (PBL), which was developed to improve medical education by moving from a subject and lecture-based curriculum to an interdisciplinary one guided by *real-life* problems. The primary learning outcomes that PBL achieved were to improve critical thinking, self-directed learning, communication, and interdisciplinary collaboration, enhance ability to contribute to a team, and develop life long learning skills. Quantitative assessments from pre and post essay exams, clinical evaluations and the weekly and semester long PBL problems determined comprehensiveness of the student's knowledge of the concepts in the course and the student's ability to communicate an understanding of the course. Qualitative assessments from the individual papers, clinical journals, peer and course evaluations revealed that these outcomes were achieved.

INTRODUCTION

PBL has evolved from the theory that learning is a process in which the learner actively constructs information (Gijselaers, 1996). Information presented only from a lecture format is of limited use and unlikely to assist students in acquiring the desired outcomes of a baccalaureate nursing education. Yet, until recently, the predominant education theory was one in which learning meant filling students' heads with information (Bruer, 1993). This *bucket theory* assumed that students stored the given information and regurgitated it upon request.

Currently, students are known to understand and retain information based upon the relationships to pre-existing structures and information (Bruer, 1993; Bruning, Schraw & Ronning, 1995). Nursing education should adapt to this shift in understanding about how learning occurs. The challenge for nursing education has always been to develop initiatives and innovations that will prepare graduates for the rapidly changing healthcare environment. Managing patients with increasingly acute conditions requires nurses with excellent analytical, decision-making, and communication skills. Students often experience difficulty in transferring knowledge from the physical and psychosocial sciences to the clinical practice settings. Current educational objectives may be contributing to the gap between practice and

theory. Objectives, which only require memorization, recall, or basic understanding, are not preparing the students to apply knowledge in the clinical arena.

Education is too often teacher-centered, keeping the student in a passive role. Research suggests that the ability to retain knowledge does not inevitably produce a competent practitioner (Barrows & Tamblyn, 1980). Confucius is quoted as saying, "I hear and I forget; I see and I remember; I do and I understand." In PBL students act as professionals and challenge problems as they would occur in a real clinical situation with insufficient information, and a need to determine possible solutions by a given deadline. (Barrows, 1985). Nursing educators know that students learn better when actively involved in the process. Most nursing courses have a clinical (hands on) experience built into the course requirements. Yet, educators have continued to focus on imparting only knowledge in the classroom setting.

For over ten years the nursing literature has underscored the need for a curriculum revolution in nursing education, emphasizing innovative strategies which allow for the socialization of a student as a colleague and professional (Butterfield, 1990; Frost, 1996; Heliker, 1994). Nursing students become socialized in to the skill needed in professional practice through valuing learning, acquiring and accepting information from other sources, critically questioning others, and obtaining feedback on learning outcomes through self, faculty and peer evaluations. (Heliker, 1994). It is in the process of encountering and evaluating real life problems that students learn both content and critical thinking.

The educational philosophy of problem-based learning (PBL) is centered on the belief that students should be actively involved in the process of learning (Barrow & Tamblyn, 1980). PBL is an exciting alternative to the more traditional lecture approach. PBL allows the students to use real-life problems to identify what they know, what they do not know, what other information is needed, where to find that information, how to analyze it, and how to communicate that information to others. The PBL approach is a systematic way of helping students to comprehend the problems of complex situations and to use experience, resources, and theoretical knowledge in solving problems, communicating and collaborating within interdisciplinary fields. By focusing on real-life problems, feedback, class discussion and student reporting, the classroom is transformed into a vibrant, active learning environment. As health care increases its dependence on technology and genetic research in order to serve a more varied cultural, racial, religious, and aged population, nursing must demonstrate competence in several key areas: critical thinking, communication, assessment, and technical skills. PBL integrated real-life practice problems into the academic aspects of instruction which brought new life to the classroom.

METHODS

In redesigning this course to the PBL format, the research question to be answered was; does the PBL methodology improve or achieve the stated learning outcomes? The learning outcomes to improve critical thinking, self-directed learning, communication, interdisciplinary collaboration skills, enhance ability to contribute to a team and develop life-long leaning ability. PBL was first introduced in the nursing curriculum in Community

Health Nursing, which is a required nursing course in the baccalaureate and post RN mobility programs in the School of Nursing. It is offered the final semester of the senior year and is a co-requisite with the Management and Senior Seminar courses. There were 24 students in the class, 23 females and one male and all were licensed RN's. The age range was 19-49 years. All of the students were full-time students, Caucasian and English speaking. The majority of the students had between a 3.0- 4.0 grade point average and expected to make an A or B in the course. A pre and post PBL assessment was done to evaluate learning styles of these students prior to experiencing PBL.

The course met one day a week for a three hours of class with each student scheduling 9 hours a week of clinical practice in a designated community setting. Clinical opportunities occurred in a variety of settings with all students sharing the common experiences of home visits through the public health department, a school-based clinic, a homeless clinic, and the AIDS clinic.

Introduction of the class content began with a discussion of course requirements and expectations. Class content was outlined in the course syllabus. A definition of PBL as well as the process was explained to the students in the first class. Particular attention was given to the differences in PBL group work and previous nursing courses' group involvement. Students were then randomly assigned to one of four groups for the weekly and semester long PBL activities.

Two faculty acted as facilitators in the class for the groups. Although both faculty were community health clinical nurse specialists, only one had extensive training and knowledge of the PBL process. During a typical class day's first hour, a mini lecture, short video, slides, guest speaker, group or panel discussion were utilized to introduce a specific topic. Prior to the class, all students were expected to review the assigned readings and be prepared to interact in class. In the second hour of class, a real-life problem was introduced and the students worked in their respective groups to solve the problem. Resources available to the students during the class included a practitioner appropriate for the day's topic, a computer lab with Internet access located within the School of Nursing, and a mini-library consisting of current textbooks and journals from community health nursing as well as from the areas of microbiology, pathophysiology, nursing management, pediatrics, adult health, mental health, and obstetrical nursing.

Problems distributed in class were developed from actual practice situations and based upon theoretical content. Frequently, these problems correlated with the students' own clinical experiences. Tutorial guides outlining key components and solutions for each problem were developed for the facilitators with each of the four modules. The four modules were carbon monoxide poisoning of a family, food borne illness outbreak involving 200 individuals, a bacterial infection, and a natural disaster.

One of the most well received and highly rated of the in-class problems was one on disasters. A few months prior to the start of the class, a level F4 tornado came within ten miles of the university. Having students in the class who had cared for or knew someone injured in the disaster highlighted the actual and potential of the disaster problem. Many students expressed appreciation for this module and said that they knew that this was a real problem they would encounter. This module, designed to be done in one class, could

be expanded to become a weeklong PBL activity. A summary of this class problem is listed below.

You are an emergency nurse in a hospital in a large medical center. Security reports that a tornado warning has been issued for the area. The Emergency Medical Service phone rings and you receive a report that there are multiple injuries reported from a tornado on the ground ten miles from the hospital. Twenty minutes later, the phone rings and your emergency department is to receive the following patients within 3-5 minutes.

Using the aforementioned information, five patient scenarios were then presented. In a ten-minute period, each group must prioritize the patients. Upon reconvening, an emergency nurse acting as the one of the facilitators had each group justify their decisions. In the second half of the problem, information on the two more serious patients was given as to their respective presentation in an emergency department. Within each group, students evaluated prior decisions and determined what additional questions, data, resources, and interventions would be required. Thirty minutes was allowed for the evaluation and upon completion, each group discussed and defended their position on the problem.

Sixty-five percent of the course was derived from group PBL activities. Fifteen percent of this was attributed to in-class problems and the remaining fifty percent involved a semester-long community project. The rest of the course assignments were individual student work and included clinical journals (10%), a natural history paper on a selected problem or disease (10%), and a comprehensive exam (15%). Due to the commitment by faculty and the knowledge that these particular students would soon be practicing in settings involving interdisciplinary teams, PBL comprised the majority of the course. Indeed with PBL, each student has the opportunity to be an active member of a team and work toward a common goal.

Assessment of student work was performed using an adaptation of the tool developed by Amos and White, 1998 which evaluated the student's quality of work, content/process knowledge, application to practice, group participation, and ability to abide by the rules of trust. Quality of work was determined by the organization, timeliness and accuracy of submitted work. Content/Process involved the balancing of the learning process through oral and written assignments. Application to practice involved demonstrating the ability to synthesize and apply learning to other practice areas and populations. Facilitators evaluated the group participation paying particular attention to a student's activities, critiques discussion and application of learning. The Rules of Trust involved the peer-evaluation component. An example of the rules of trust is displayed in Table I. Each student evaluated every other member in the group. The peer evaluation comprised one fifth of the evaluation on each problem. The group members decided what criteria were to be evaluated for the rules of trust.

SEMESTER-LONG PBL PROJECT

As previously noted, a large component of the PBL evaluation involved a community- management project. For this project, students were assigned to a different

group. Similar to the weekly groups, each group consisted of four to five students. These groups functioned separately and independently of the weekly PBL groups. The emphasis of the PBL Project was to enhance students' creativity and critical thinking. Each group was assigned a real-life problem in a selected community.

Table I. Rules of Trust.

Team Member________________ Peer Evaluator____________

Problem: ____

Rate each person in your group on a scale of one to five on the following behaviors. Circle your response. The scale is:

1- Poor 2- Below Average 3-Average 4- Above Average 5-Excellent

1. Participated as an active group member	1	2	3	4	5
2. Followed through on individual tasks	1	2	3	4	5
3. Collaborated in the planning process	1	2	3	4	5
4. Participated in oral presentation	1	2	3	4	5
5. Participated in completion of the final written product	1	2	3	4	5

Please check the primary roles of the team member you are evaluating.

Leader_____ Writer_____ Researcher_____ Planner_____ Presenter_____ Creator_____

Other Roles Describe:____

____

____

The course coordinator along with a community representative confirmed the problem to be addressed prior to the onset of the project. For the purpose of the project, a community was defined as "an open social system characterized by people in a place over time who have common goals" (Smith & Maurer, 2000, p. 342). The communities selected for the projects were a small city, a school-based clinic, a homeless clinic, a multi-cultural

elementary school, a diagnostic center in a major hospital, and an outpatient/surgical center for children. The specific goals of the project were to:

- Describe the problems of the community
- Identify the potential and actual resources available to the identified patient (s) in the problem or others seeking care in the community.
- Develop a systematic method for identifying the health, environmental, management and social issues in the community.
- Analyze morbidity, demographic, and healthcare issues that are affecting the community and its members.
- Describe the community's management style including organizational structure, funding sources, and budget.
- Analyze the gaps and barriers in resources.
- Recommend solutions for the identified problems.

Ample clinical time was allotted for the student groups to gather the needed information through computer and library searches, Centers for Disease Control (CDC) and Vital Statistics data, community visits, and community officials interviews. Over the next several weeks, group members took responsibility for completing identified tasks. Facilitators met weekly with the groups to assess progress and offer feedback. We approached this activity from the philosophy of Philip C. Schlechty who stated." learning involves action; most of what students learn comes from what they do which includes listening, creating and talking; regardless of the mode or style of learning, it is what students do and the meaning they give to it that determines what they learn." (Schlechty, 1997, 42).

At the end of the semester, each group presented their findings in a written formal paper as well as a professional poster. The poster was presented with an oral defense to peers, faculty, other nurses, an external nursing consultant, and invited guests from the specific communities. The findings presented on the poster and in the paper included justification on the basis of research which permitted the course faculty to evaluate the students' understanding of the parameters of the designed problem. The poster presentation allowed the students to discuss and display their data and interpretations one-on-one in a small group atmosphere. (Fortner, Bisson and Loretz, 1998)

RESULTS

Evaluation guidelines for individual work of the natural history paper, peer review of the paper, pre and post essay exams, clinical requirements, and facilitator evaluation of student and clinical journals were given to each student. All these activities were graded. Quantitative evaluations were obtained through a pre and post-content essay exam given to all students and the Health Education Systems, Inc. (HESI) exam (Lauchner & Britt, 1998) which is a 160 item comprehensive multiple choice test with critical thinking items similar to those on the national licensure exam. The HESI test is designed so that the test taker must use critical thinking skills to answer the questions correctly. This exam was given at the beginning and end of the term. Although this exam was graded, the score was not computed

in the grade for the course. It was expected that increased test scores would be the product of the PBL course given the strong emphasis placed on critical thinking skills.

The HESI revealed increases in all areas (Table II). There were significant increases in the probability scores from the pretest to the posttest ($p = .001$). Areas that increased of particular interest to this included: analysis from 88.75 to 99; reduce risk potential from 83.70 to 96.35. This may be due to the strong clinical application component of this course in areas of public health, home care, homelessness and school health.

Table II. Health Education System, Inc. HESI Results Comparison of Pre and Post Class Probability Scores In Selected Categories Relevant to Community Health Nursing.

Category	Pre Class Score	Post Class Score
Assessment	89.67	95.45
Analysis	88.75	99.00
Planning	88.82	99.00
Implementation	83.54	94.45
Physiologic Integrity	88.71	99.00
Medical/Surgical	91.18	99.00
Pediatric	87.10	99.00
Gerontological	77.10	89.90
Reduce Risk Potential	83.70	96.35
Basic Care and/Comfort	76.92	99.00
Pharmacologic/Parental Tx	94.63	99.00
Physiologic Adaptation	90.31	99.00
Coping and Adaptation	80.41	89.95
Prevention and Detection of Disease	81.24	97.13

Students completed a Student Attitudes and Activities Assessment (SAAA) developed and provided by an external assessor. This tool examined student's attitudes toward a variety of teaching and learning strategies. A Likert scale from 1-5, strongly agree to strongly disagree was used to grade responses. Students participating from the School of Nursing showed little attitude differences between the onset and completion of the course for

the majority of attitude items. This observation may be attributed to the fact that these groups of students were all registered nurses with a variety of experiences and previous exposure to group work and interdisciplinary collaboration. Of those students who did not have work experience, all had medical mission experience in Africa and/or Venezuela. Regarding specific items from the SAAA, for item 9, "I feel comfortable working and participating in small groups"; there was no change. Students were comfortable with

group/team work at the beginning and end of the course. This finding is not surprising considering that these nursing students have had many opportunities in the nursing curriculum and in life or work experiences to participate in group/teamwork.

Also, perhaps because of their maturity level and work experience, students did not expect that the teacher would be primarily responsible for their learning in the beginning or at the end of the semester. An additional item of interest was item 11; "I feel the instruction of this course is similar to other classes that I have taken at Samford." For this item, students' attitudes changed. At the end of the semester, students indicated that this PBL course was not similar to other classes taken at Samford. Even though group work had been a part of previous courses, it was had not been for an entire semester and the format of the other courses were still primarily lecture/discussion.

An additional tool used to assess students in this class was one that the nursing PBL team developed. This tool was a twenty-three item pre- PBL survey, which was completed in the spring by all the students who were scheduled to take Community Health Nursing the following fall. The survey assessed demographic information, perception of group work, styles of learning, and preferred method of evaluation. At the end of the fall term, the students were given the survey again to determine if their perceptions, styles of learning or preferences. Overall the descriptive findings were similar at the beginning and end of the semester for reasons previously stated. There was a significant difference ($p=.0067$) in the pre and post results for item 11, "I find the teaching/learning method of case studies to be not helpful to extremely helpful." In the pre-assessment, only 63.2% thought case studies were helpful to extremely helpful. In post assessment, 95% found case studies to be helpful to extremely helpful. One student (5%) felt case studies were only somewhat helpful.

Student evaluation of PBL was obtained through qualitative data at mid-semester, after the semester long project and at the end of the course. Qualitative data was obtained with the open-ended question, "What did you learn from this PBL experience?" These comments were reviewed for key words such as group/teamwork, critical thinking, leadership, and application of learning, and categorized. These findings are reported as frequencies in Figure 1. Comparisons were made in mid semester, project and end of course responses. The number of varied comments increased as did the number of categories. All students at the end of the term responded that they had learned more about team/group work.

The assignment of the journaling gave the students the opportunity to describe patient problems, use critical thinking, and collaborative interventions throughout the semester. The faculty in the course also did journaling. The journals validated the PBL process through the students ability to problem solve in the clinical setting. Creedy and Hand (1994) recommend that PBL faculty keep a reflective journal after PBL sessions. This allowed the faculty to explore their evolving personal reflections as the course progressed.

DISCUSSION

As nursing educators with a variety of teaching experiences with students from varied backgrounds and educational level, we considered ourselves to be innovative and

creative educators. Yet, no other active strategy has produced the results we received with PBL. There was nothing to stifle the students' thoughts, ideas, or comments from freely flowing into the learning environment.

Students, that were passive in previous courses, began talking, volunteering to do Internet searches, asking thoughtful questions, leading small group discussions, and reporting valuable findings on a weekly basis. This finding was most evident in the semester long project. In previous courses, group work had been a part of the course but never with the same people working on the same problem for this long an interval. By being a part of the same group for three months, the students developed much more than problem- solving skills. In their own words, they related: "that a diverse group can complete a project we can all be proud of by using teamwork;" "to delegate and accept responsibility;" "to work as a team."

Others internalized the process reflecting more of a self-assessment during this process indicating personal and professional growth. Comments included: "differences can be resolved in a civil manner;" "it is important to communicate on a personal level." " I was challenged to think in class;" and "it is important to be open-minded and willing to admit I may be wrong."

The placement of this PBL experience in the final semester of the senior year was positive in a way that was not foreseen. The nursing curriculum was a natural fit to PBL. For one, there was no shortage of interesting, real-life problems. Second, the students had a base of knowledge from which to draw from and apply PBL principles in an entirely new setting. Students also sought out professional meetings such as the National Conference on Undergraduate Research (NCUR) and were accepted to present. Many students were encouraged and inspired to pursue graduate study based upon the evaluations of these PBL projects. Of the 24 students, eight students enrolled in graduate study and five more have been accepted.

The assertion to be proven in redesigning this course to PBL was that this new methodology could improve and achieve learning outcomes. Findings support PBL, as a strategy that allows students to achieve the learning outcomes of this course. As the final senior level course for baccalaureate students, the course objectives were designed to prepare them to go out into the real world and practice as professional nurses. The Essentials of Baccalaureate Education (1998) recommend that graduates have these core competencies: critical thinking, communication. assessment, and technical skills. Core knowledge is expected in health promotion, risk reduction, disease prevention and management, ethics, diversity, global health care, heath care systems and technology.

Results as reported in Table II and Figure I support that PBL improved learning outcomes and achieved these core competencies. In addition, the students' prior education, life, and work experiences combined with the opportunity to apply this knowledge through weekly PBL activities, the PBL semester long project and the clinical experiences also supported that this methodology improved learning outcomes.

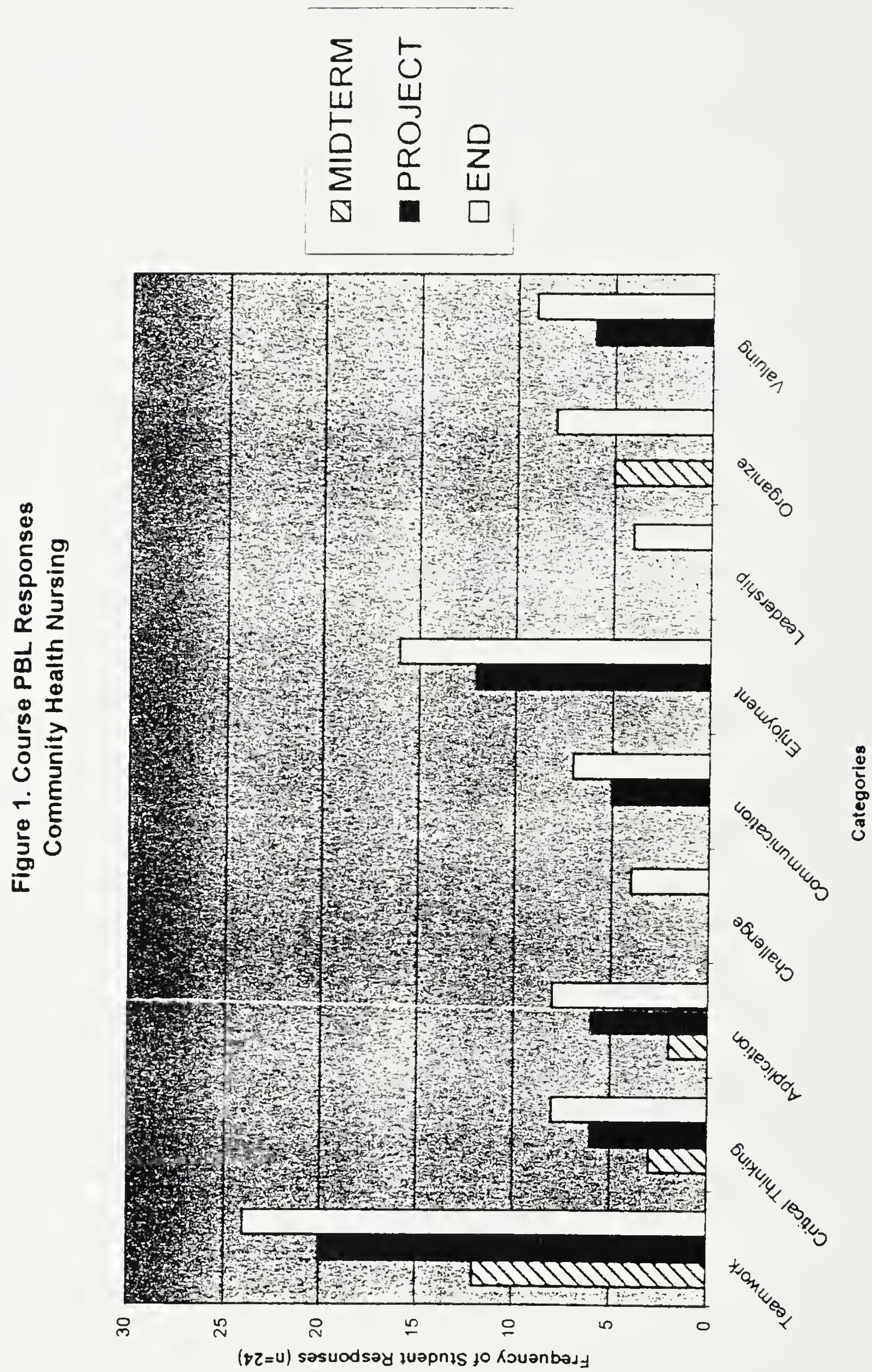
Figure 1. Course PBL Responses
Community Health Nursing
MIDTERM
PROJECT
END
Frequency of Student Responses (n=24)
30
25
20
15
10
5
0
Teamwork
Critical Thinking
Application
Challenge
Communication
Enjoyment
Leadership
Organize
Valuing
Categories

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PROBLEM-BASED LEARNING IN A SCIENTIFIC METHODS COURSE FOR NON-SCIENCE MAJORS

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ABSTRACT

Non-science majors frequently fear science and have misunderstandings about how science is carried out. By using case-based and problem-based approaches, students seek information on relevant, modern topics in science. Following intensive instruction and practice in scientific methods, students in this course were given a variety of problems that addressed various aspects of science, including genetic modification of plants and some of the ethical issues of AIDS. Groups of students then responded to each problem using a variety of means including literature reviews, position papers, simulated letters, and mock debates. Assessment of attitudes and knowledge indicated that problem-based approaches reflected an improvement in both aptitude and attitude toward science. Active learning processes ideally will equip and promote students' life-long learning about complex issues in science in the future.

INTRODUCTION

Because the United States is an international leader in scientific research, the public has long assumed that undergraduate education in science serves all. Yet many national concerns have attended this status, as many citizens have lagged behind in awareness, knowledge, and attitudes toward science. As David Goodstein has written, "the United States has, simultaneously and paradoxically, produced both the best scientists and the most scientifically illiterate young people" (Goodstein, 1993). Furthermore, the population of women and minorities has been underrepresented traditionally in the scientific disciplines. In *The Liberal Art of Science*, the American Association for the Advancement of Science states that scientific discovery "involves active engagement with the natural world and social interaction among the members of community of scholars (*AAAS*, 1990).

These national concerns are recognized locally in the attitudes and aptitudes of Samford students. Many students seek to take only those courses that are perceived to be the "easiest" science courses, and they describe themselves as bored by science classes. Furthermore, although women make up over 60 percent of the freshman class, fewer than half of the majors in biology, chemistry, and physics are female.

Samford students in discipline-specific courses for non-science majors appear to lack understanding about how science is carried out. Both science majors and non-majors tend to memorize facts reasonably well but do poorly when asked to reason through problems. Further, many students may have retained some knowledge from their high school science courses, but they have little concept of how scientific findings originate and are conveyed to others. At Samford we see that science majors have difficulties designing experiments, and their discipline-specific courses emphasize coverage more than process. Comprehensive coverage of discipline-specific material is important for science majors, but students rarely work directly with that knowledge in their scientific careers. The skills we attempt to address in this course, such as the ability to think critically, to approach complex problems with collaborators, and to use scientific methods to propose explanations and solutions, will better equip students for excellence in their occupations. But perhaps an even greater benefit is the education of future teachers, business leaders, politicians, and attorneys. These individuals, whether in their careers or as voters, will be the primary shapers of the direction of scientific research for the future. It is vital to have students learn "by direct experience with the methods and processes of inquiry" (Advisory Committee to the National Science Foundation, 1996).

Samford students also lack perception of the connections between the science disciplines. This lack of perception is present in both science majors and students with other majors, even though we have made conscious efforts to teach interdisciplinary science. For example, an alternative core curriculum, Cornerstone, was developed at Samford and emphasized interdisciplinary learning in the arts, humanities, and science. This pilot program is the model for the Scientific Methods course. In the Cornerstone science course, 14-20 students carried out classic experiments, such as measuring the gravitational constant, and original research, such as measuring the effect of ultraviolet light on snail embryos and the masculinization of mosquito fish due to environmental steroids. Students now take the Scientific Methods course (one semester with no laboratory) followed by a one semester course in a laboratory science. The Cornerstone program serves as a model of how interdisciplinary learning can work, and these principles have been used to redesign the core and general education curricula at Samford.

Samford non-science majors demonstrate an overall negative attitude toward science, as exemplified by comments from students. Many students have a phobia toward science that is reflected in their grades and even more in their attitudes. By emphasizing the process of science, rather than the inundation of specific facts, we can eliminate the fear of science that many students bring with them. We can also alleviate the general disdain for science expressed by some students, who find science dull, repetitive, dehumanizing, and irrelevant to their lives. These students often condemn science for contributing to many of the world's problems, from the atomic bomb to chemical and biological warfare. Obviously, change is needed to ensure that the United States has citizens who understand the important role of science in social and political contexts. We feel that Problem-Based Learning (PBL) and other active learning strategies can aid in this change in attitudes toward science.

Traditionally, research institutions have played a central role in scientific education. However, research institutions often must work against the prevailing academic climate in order to accomplish necessary reforms. For this reason, as Daniel Sullivan, President of Allegheny College, has noted, "the nation's liberal arts colleges . . . are fertile soil for

innovation and experimentation" (Sullivan *Reengineering Science Education*, 1994). Samford's faculty in biology, chemistry, and physics have worked cooperatively to restructure the undergraduate science requirements and to develop an innovative, interdisciplinary core course in science.

THE ROLE OF PBL

Problem-based learning is effective in changing student attitudes and in guiding student learning (Duch, 1996). Once students see that the best scientists (and the best science students) are not the ones who have memorized the most facts but are the ones who apply those facts in the most creative manner, we will have gone a long way toward conveying what science does. Science is, in fact, a problem-solving discipline, and we must shift the paradigm from the accumulation of facts to problem-solving, and PBL can help accomplish this. This shift could help show students how science affects their lives, for they will rarely be asked to regurgitate previously mastered scientific facts.

Further, PBL addresses the shortcomings of science teaching identified by the AAAS and other bodies. Specifically, PBL involves the use of work within small groups, promotes lifelong learning, provides context for science in students' lives, and identifies the connections between scientific disciplines (Allen, 1996). Once students see the mechanics and creativity of science, they can become better consumers of scientific information and more informed citizens in the decision-making process concerning science.

HISTORY, OBJECTIVES, AND INSTRUCTIONAL METHODS OF THE COURSE

This course was originally conceived as a course for all non-science majors at Samford; it now serves as one of several science courses students can take to meet their science requirement. Since the course has as its knowledge base all of astronomy, physics, chemistry, and biology, the emphasis was shifted away from memorizing facts toward the process of science. There are several sections of the course taught each semester by professors in the Departments of Physics, Chemistry, and Biology.

The objectives of the course are 1) to comprehend methods scientists use to explain the natural world, 2) to employ popular scientific magazines and journals to investigate current questions in science, 3) to contrast science with pseudoscience, 4) to relate the scientific method with modern topics in the basic sciences, and 5) to appreciate the role of science in the modern world. The course developers felt that students could meet these objectives best by investigating problems in small groups.

Students also use a variety of methods to communicate their findings to their classmates. Presentations consist of short, focused writing assignments, brief talks to the class, and posters presented to the class. Students are reminded of the importance of communication in science and thus demonstrate that communication in the same ways that scientists present. Where possible, other faculty members aid in grading to simulate the peer review process.

The initial segment of the course was an introduction to PBL and to scientific methods. Students worked in groups to design experiments and acted as subjects for investigations into pseudoscience. During this time, students became familiar with the other members of their group and the learning styles of the individual members. The class then received a series of

problems that get progressively broader as the semester progresses.

Famous scientists and the scientific method

In this problem student groups were asked to take the role of student teachers delivering a talk about scientific methods to a high school science class. One person from each group presented an overhead of a famous scientist and explained how his or her experiment met the criteria of science (hypothesis, prediction, results, etc.).

Cloning animals

Student groups assumed the roles of Congressional aides in this problem. They were asked to generate a short literature review on the subject of cloning animals as well as generating ten questions (and answers) that the Congresswoman will ask of a scientist interested in doing animal cloning. Students learned to assess the quality of sources and the value of a literature review to supply the state of the art in a subject.

Fast, fun physics

This problem, adapted from Dr. Ben Still of Clemson University, gave students an opportunity to gain hands-on experience. All groups completed a series of eight simple exercises, and then one group was chosen to teach the class the physics behind each one. Many of the students were able to find the appropriate formulas in physics textbooks. This problem also gave students the experience of presenting information orally before a class.

To kill or not to kill, that is the question

Student groups debated whether to destroy the remaining stocks of smallpox virus, currently stored in Russia and the United States. Groups were presented with a little information at first, and they generated a list of questions. They then received a little more information and determined how to make their decisions. Student groups wanted to know what uses of the virus stocks there might be and how secure the vials are from theft or political use. They wrote their findings after investigating the pros and cons of each decision.

Playing God in the garden

Student groups were given an article from the New York *Times* magazine section from October, 1998 about genetically modified plants. They then wrote a position paper, as a group, on whether genetic engineering in plants should have more regulation. This exercise also had students conduct polls of their classmates or grocery shoppers to determine their opinions on the matter. Students learned that genetic engineering has important benefits as well as serious concerns. They also found that produce managers at local grocery store chains are generally uninformed as to whether they receive genetically modified food or not.

Too many vaccines?

Students were given a scenario involving the birth of a child and the decision as to whether the child should receive the entire battery of childhood immunizations. Students generated questions as to the safety and effectiveness of vaccines and seek a variety of opinions in forming their opinions. Groups wrote their findings and the reasons for their decisions.

AIDS, HIV, NEP's, and IDU's

In this problem, student groups received a little information about the severity of HIV and AIDS among intravenous drug users (IDU's). The students were asked to think of ways that HIV and AIDS can be decreased among this population. They were then told of needle exchange programs (NEP's) that give sterile syringes and needles to drug addicts who bring in used syringes and needles. Student groups were randomly assigned a variety of roles (scientist, drug treatment officials, addicts, politicians, e.g.) and debated whether the federal government should fully fund needle exchange programs in cities where there are a lot of IDU's. Student groups were not told which position they should take on the issue and are allowed to question each other. One person from each group was selected as spokesperson, though the entire group developed the argument. Students were reminded that their opinions alone are not important in science–they must back their opinions with data. Students came to appreciate the difficulties in working with human subjects and the limitations of scientific research. The decision about federal funding is not made by scientists, but is made by politicians.

Low-carbo loading

Surveys show that a high percentage of people will be on a diet at some point in their life, and dieting is very common on college campuses. Students were given a conversation between college students about the low carbohydrate diet and are asked to determine if the diet is safe and effective. The student groups turned in a short paper about their findings and were given explicit instructions about identifying whether their sources are primary or secondary and whether they were biased or not. Students will ideally use this experience to identify whether other popular diets are beneficial or not.

Playground of science

Finally, students were asked to design playground equipment for a fictitious school of math and science. Each group's design was to demonstrate some aspect of science or mathematics and was to be safe, fun, and relatively inexpensive. Presentations were done as posters, and each group presented to the rest of the class.

ASSESSMENT

Assessment was conducted on group and individual bases. Each group's presentation of a problem was graded and individual scores determined based on the group's assessment of each member. Group scores accounted for 70% of the grade of each student with the rest of the grade determined by individual test results; where possible, colleagues also graded the presentations to simulate peer review and to provide another point of view. In order to assess the working of each group, objective, machine-graded tests were given to each student and then the same test was given to each group. Members of the group turned in a single answer sheet and all sheets, individual and group, were graded at the same time. This method of testing gave students immediate feedback on their performance and also allowed them to see that the group almost always scored better than individual students. Students were responsible for the general

information presented for each problem which constituted most of the depth of the course. In addition, students were continually tested on the basics of scientific methods to reinforce the objectives of the course.

RESULTS

While there is ongoing assessment of the effectiveness of PBL, some preliminary work indicates how well this course meets its objectives. Figure 1 shows preliminary results taken from the author's section (31 respondents) of the course in the fall of 1999. These results indicate that students, in general, were meeting the goals of PBL in this particular course by learning to solve real world problems, by identifying appropriate resources for non-science majors and by taking an active role in their own learning. Also notable are that students reported being able to work well in teams and used materials and concepts from outside the course to complete assignments.

Figure 2 indicates how well all sections of the course during the fall of 1999 met the course objectives (112 respondents). This survey indicates that we have more work to do in having students meet the course objectives, but the results are still generally positive. Problems can and will be designed to address the weakest of these goals, recognizing the difference between science and pseudoscience, for example, and improving the attitudes of students toward science.

Of potentially greater concern are the results shown in Figure 3. This survey of all students in the course during the fall of 1999 (N= 112) was designed to measure attitudes and activities of students. There are positive aspects of the survey in that students report regular attendance and participation in problems, but the survey also shows that students still do not like to read or discuss scientific articles and show some reluctance to work in groups. These results may lead to changes in the amount of group work done in the course. Students are, however, reminded that their careers will likely involve working in groups and getting undue credit and blame for their efforts.

CONCLUSIONS

Problem- and inquiry-based learning techniques provide effective tools for student learning. Students who admit to little interest in scientific matters outside of class report satisfaction working in small groups on problems in science. A large percentage of students also indicate that they attend class regularly and actively participate. Furthermore, the students generally state that they met the course objectives of understanding how science works and its characteristics. The timeliness and interest level of modern scientific topics make them ideal for stimulating active learning in non-science majors. Students also learn to cooperate in groups and learn presentation skills, as the answers to problems are presented in written, oral, and poster forms.

One additional benefit to inquiry-based or problem-based learning is the stimulation of lifelong learning. Since students seek answers to questions in scientific literature designed for them as non-scientists, they can call on the same resources to find the answers to questions in the future. Real world problems are used where possible to assist in this process as well as to

show the relevance of science to non-science majors. Learning paradigms such as these may help the country as a whole to meet the goals of more effective science instruction and a better educated populace.

Finally, PBL allows more creativity for the instructors. Professors are free to explore neglected, but important, areas of their discipline that lie outside their expertise. By having students be responsible for their own learning, instructors are no longer tied to their lecture notes from previous years. Instructors act to motivate and guide, rather than act as the center of the learning process (Allen, 1996). Also instructors then become the model of lifelong learners as they explore areas of science outside their discipline. Hearing science instructors admit that they don't have all the answers can lead students to an understanding of the exciting nature of science as well as its joy and the awe it inspires by its ability to address problems that affect everyday life.

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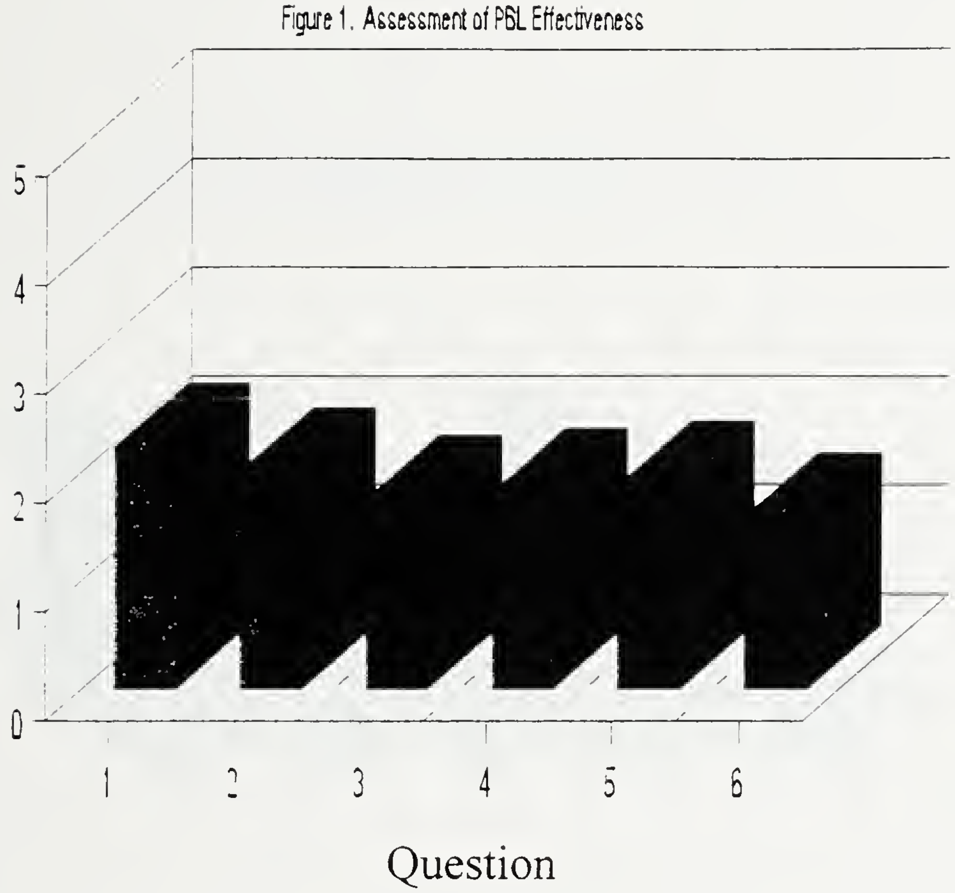
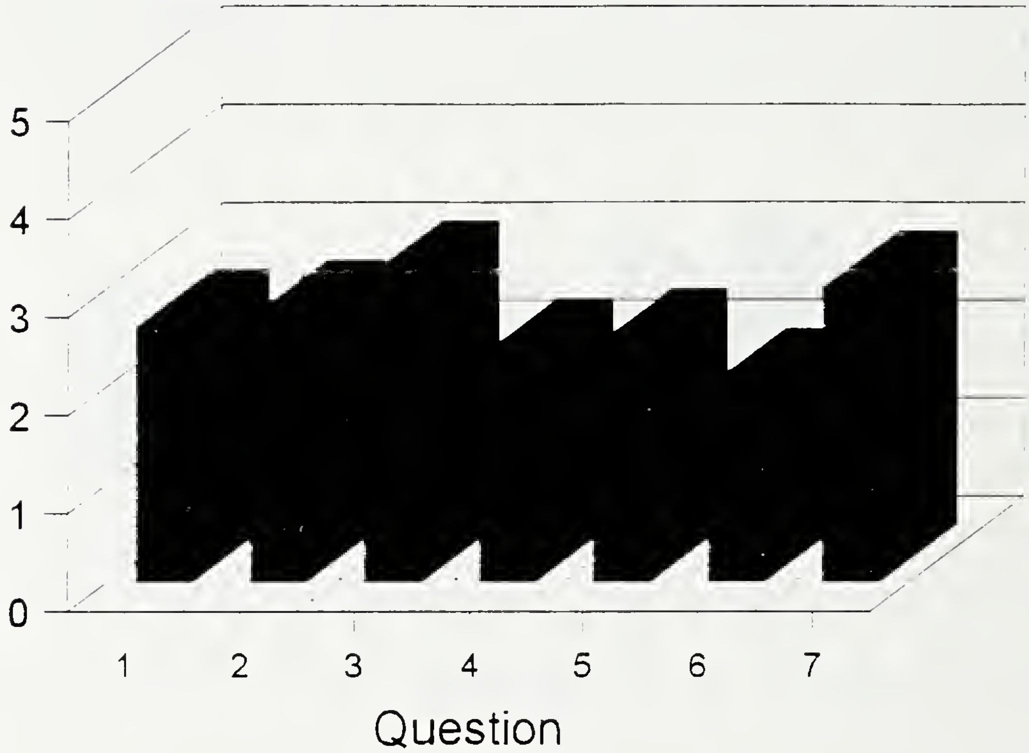


1 = Strongly Agree; 2= Agree; 3 = No Opinion; 4 = Disagree; 5 = Strongly Disagree

1. This course increased my ability to solve real-world problems.
2. This course encouraged me to consider alternatives when solving problems.
3. This course improved my ability to identify appropriate resources.
4. This course increased my ability to work effectively on a team.
5. This course encouraged me to take an active role in my learning.
6. I have used knowledge and methods drawn from outside this course to complete my course assignments.

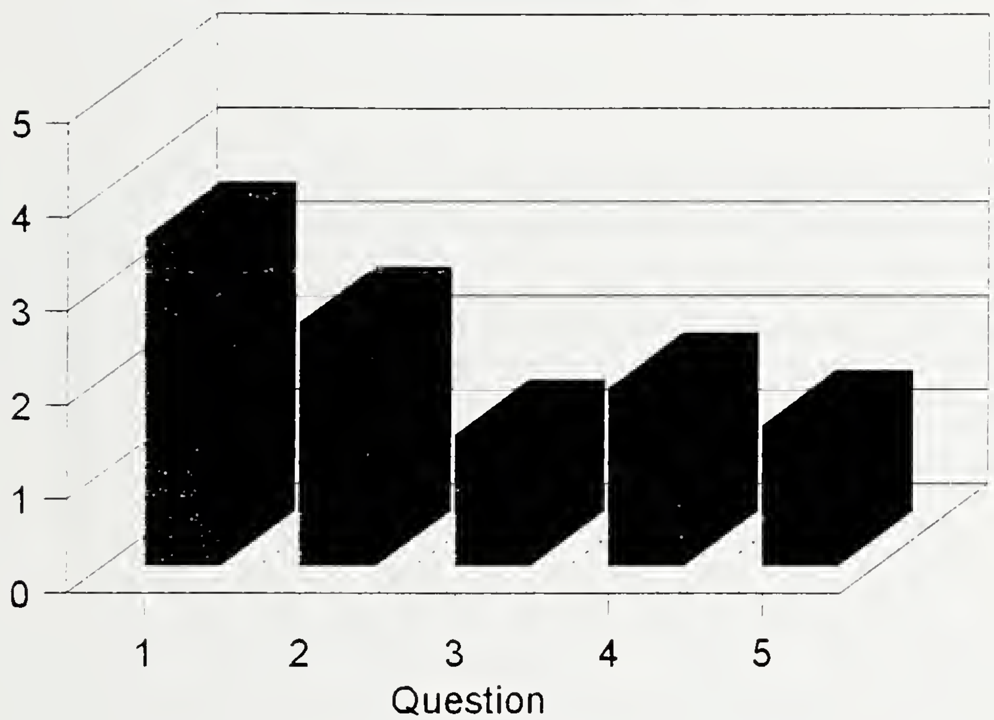
Figure 2. Assessment of Course Objectives



1 = Strongly Agree; 2= Agree; 3 = No Opinion; 4 = Disagree; 5 = Strongly Disagree

1. I have learned to comprehend the methods scientists use to explain the natural world.
2. I have learned to employ scientific magazines and journals to find answers to current questions in science.
3. I can now contrast science with pseudoscience.
4. I can relate the scientific method with modern topics in the basic sciences.
5. I have learned to appreciate the role of science in the real world.
6. The class was successful in changing the lecture format (professor didn't lecture too much).
7. My attitudes about science have changed as a result of taking this course.

Figure 3. Student Attitudes and Activities Survey



1 = Strongly Agree; 2= Agree; 3 = No Opinion; 4 = Disagree; 5 = Strongly Disagree

1. I like to read scientific articles and discuss them with others.
2. I liked working with others in the course on group assignments.
3. I have attended class regularly and have been an active participant.
4. I was well prepared for this course by my high school or previous studies.
5. My grade average in this course so far is: 1=A, 2=B, 3=C, 4=D, 5=F

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COPING WITH COURSE CONTENT DEMANDS IN A PROBLEM-BASED LEARNING ENVIRONMENT

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ABSTRACT

This paper examines the issue of course content demands in a Problem-based Learning (PBL) environment and discusses methods and approaches designed to address the problem. While course content demands are often seen as a logistical issue, this paper argues that the problem of course content demand may also be viewed in the context of broader theoretical challenges that involve both course design and instructional philosophy. Also discussed are two techniques that can be used to meet course content demands in a PBL class. These techniques can lead to similar learning outcomes as PBL is designed to accomplish and therefore are useful alternatives to conventional PBL modules.

INTRODUCTION

Problem-based Learning (PBL) is a time-hungry method of learning. Class time, once reserved for lectures, must be exchanged for group problem-solving activities. The tension between the time demands of the method and the disciplinary demands of a course is one impediment to PBL implementation. In this paper, we start with an examination of the issue of course content demands. We argue that PBL practitioners, and perhaps all educators, need to find a balance between the breadth of material covered in a course and learning effectiveness, as neither learning effectiveness nor teaching quality can be equated with the sheer volume of information delivered. However, we recognize that in some cases the instructor has to cover a specific amount of information within a limited amount of time. Therefore, two of the techniques that can meet course content demands are discussed in the second half of the paper.

COURSE CONTENT DEMANDS

Every instructor has agonized over which topics to cover in a course. Course time is limited, but knowledge is limitless. Most course topics are broad enough that the instructor is faced with a huge volume of information and a finite amount of class time to deliver the material. As geographers, the authors have had to reconcile the breadth of their subject with practical, cognitive, temporal, and logistical limitations (Fournier 1999).

Course content demands are even more pressing when time-hungry techniques such as problem-based learning are employed in the classroom.

Instructors have taken a variety of approaches to this issue. Some elect to skip textbook chapters that are deemed less significant or unsuited to the students' level. Others emphasize a study of key concepts in lieu of a massive volume of facts. In some cases departments may develop a consensus on a core set of knowledge for a particular class; in other cases, course content may be driven by the position of a course in a sequence (for example, an introductory course that is a requirement for an upper-level class) or by the needs of students to pass professional qualifying examinations.

For most part, decision on what to cover is a problem of logistics, as one struggles to find a balance point between the greatest coverage of material and the maximum ability of students to absorb that information—all within very real time constraints. Nonetheless, the anxious question: '*Have I covered enough?*' never really goes away. New, inexperienced teachers typically suffer from this anxiety or agony. As they accumulate experiences, they either learn to communicate more efficiently, or begin to see the programmatic boundaries of course content and learn to live with that (Andrus & Tavakkol 1996). Except for circumstances where a standard curriculum is employed, most instructors can single-handedly determine what to teach in their own courses. Thus, what we have called course content demand typically emerges from an instructor's self-imposed sense of responsibility rather than from any outside sanctioning group.

Most faculty members realize that true learning is about understanding rather than the memorization of facts. With such a content-driven approach, memorization of facts is stressed, rather than the development of conceptual understanding (Allen, Duch, & Groh 1996). Still, most students equate knowledge with information (Burch 1995).

A LOGISTIC PROBLEM OR A PHILOSOPHICAL ARGUMENT

The tradeoff between breadth and depth in a course is both logistical and philosophical. Just as some educators attempt to cover as much ground as possible in a course, others may believe in trading breadth for deeper learning. It is difficult to judge which approach is better due to the difference in underlying premises. No other method is more efficient in delivering information than lecturing. The key reason for that lies in the very fact that the instructor dictates the learning content, the pace of learning, and to a large extent, the atmosphere of learning in the lecturing style (Cashin 1985; Loxterman 1998). Nonetheless, whether lecturing is the most efficient way to learn is a different story. There is much evidence to show that it is not (Bridges 1992, Barrows 1996, Gijselaers 1996). While there are methods to improve lectures, using these methods to encourage higher order thinking skills among students remains a challenge (Bonwell 1996).

Teaching does not guarantee students' learning. Moreover, the amount of course content covered in a class does not equal to quality of teaching and has little to do with learning effectiveness. For example, Dion (1996) noted that the structure of a traditional class prevented students from seeing that the information in textbooks and lectures had been produced by years of research and inquiry. The collection of facts in the text was the product of countless inquiring spirits driven by a passion for learning and a curiosity about the world—a passion that can be doused with a deluge of facts, figures, and definitions.

In addition, courses driven by high content demands tend to emphasize lower-order thinking skills. In Bloom's (1956) well-known taxonomy of cognitive thinking, the first two levels are knowledge and comprehension. Simple recall of facts and information are the primary goals of such an approach. Higher order skills such as application, synthesis, and evaluation can only be achieved through a more active approach to learning. That is exactly where PBL comes in.

PROBLEM-BASED LEARNING

PBL is based on the idea that learning is a process in which the learner actively constructs knowledge. Research (Anderson 1985) in cognitive psychology suggests that methods that involve students as active participants in the learning process produce better results. Gijselaers (1996) summarized the literature on PBL and educational theory and identified three key principles.

1. Learning is a constructive and not a receptive process.
2. Knowing about knowing (metacognition) affects learning.
3. Social and contextual factors influence learning.

Note that none of the three principles make any specific reference to course content. Instead higher-level educational goals are promoted. One of the factors that led to the initial creation of a PBL curriculum at Canada's McMaster University was a perception that medical students were saturated with vast amounts of information that had little to do with actual medical practice (Barrows 1996).

This premise is often in direct conflict with the demands of a course. An adequate amount of time should be scheduled for students to think, to explore, and to make mistakes and then correct them (Jones, Rasmussen, & Moffitt 1997). In short, deep learning cannot take place in a hurried fashion. Besides, a PBL instructor should leave extra time for student-centered activities, of which an instructor has less control. Indeed, most PBL instructors report having difficulties covering the same amount of topics as in a traditional lecture-based class. PBL could be considered a high-risk educational strategy. Features of high-risk strategies include spontaneity, long time periods for resolution, and a lack of structure (Sutherland & Bonwell 1996). Philosophically, an instructor using the PBL method should fully understand the tradeoffs and feel comfortable with covering a lesser amount of material. Many educators agree that a course is only a starting point of learning. Much learning takes place after the class is over. After all, an instructor cannot tell students all they need to know about a subject in one single course. Hopefully, PBL can develop self-directed learning skills in students and enable them to become lifelong learners. From this point of view, the emphasis on learning skills and other learning issues is a worthy investment of class time and teachers' effort. If so, the trade of a lesser amount of course coverage for these learning skills is worth making. As Thompson (1996) notes, many students—particularly in introductory-level classes—will never be practitioners in the field in question. They have little need for content-driven instruction. But regardless of their career choice, they will need to be logical and scientific in their approach to challenges, evaluate the quality of a growing volume of data, and take positions on complex issues. This notion

rings especially true in an age where most disciplines advance at a rapid pace and the shelf life of information is often quite brief (Cowdroy & Mauffette 1998).

METHODS FOR COVERING THE BREADTH

In some cases, the pressure from course content demands is real and pressing. For example, some courses are prerequisites to more advanced courses so a certain amount of basic knowledge has to be covered. There are also courses required for students to pass a certificate exam. Under these circumstances, a responsible instructor cannot ignore course content demands and arbitrarily decide what to teach. The instructor does not have to give up the PBL approach under these constraints. There are a few course activities that one can use to address course content demands. The remainder of this paper discusses some of these methods to reconcile the time demands of PBL with the content demands of a typical class. These methods may be particularly useful in an undergraduate class where students often lack of the skills of self-directed learning.

Group Quiz

One means of reconciling the demands of an introductory level course with PBL is to employ a series of group quizzes—typically based on textbook readings. Application of this method involves presenting students with a multiple-choice quiz that they complete by themselves. Students then form into their groups and take an identical quiz. After completion of the quiz students grade them and combine the group and individual grades. By engaging in this method, students share, argue, reflect, and defend their position. As a result the quiz process becomes less a means of assessment and more of an integrated part of the learning process. It is also an efficient way to get students to read the textbook and to learn basic course content (Herried 1999; Michaelsen, Watson, & Shrader 1985). Typically quizzes are given often (once a week, once for each chapter, etc.). Eventually the technique becomes part of the class culture and can be implemented without much time lost. To accomplish this, both group and individual quizzes have time limits (in the case of one author—15 minutes for the individual portion of a 25 question quiz and 20 minutes for the group portion). While some argue that time limits increase student anxiety, reduce performance, and are especially difficult for students with certified learning disabilities (Herman 1999), they are essential to prevent this technique from taking over the class completely. These quizzes may be announced ahead of time, planned on a regular basis (for example, every Wednesday), or given unannounced as "pop quizzes" (Kauffman 1999).

Group cohesion is an important part of PBL, as most problems require group work for their resolution. This method reinforces group cohesion by placing content recall within a group context. As noted earlier, social and contextual factors can influence learning. By placing a common means of assessment such as a quiz within the social context of group learning, high-level educational objectives can be achieved (Slavin 1992). Most of the content quizzes are based on low-level thinking and simple recall, but the integration of the method into classes eventually helps student groups when they begin to tackle higher-order challenges. Students learn to defend their answers, to evaluate a variety of choices, and to draw comparisons from other facts and concepts that they have learned earlier in the class.

The method also emphasizes the benefits of group cooperation, as group scores are almost always higher than individual scores. Note that students grade their own quizzes. This provides immediate feedback as well as providing opportunities for discussion. Such a method also allows students to know how their fellow group members performed on the individual portion of the quiz. The exposure of grades in a semi-public forum may increase pressure on students to perform as well as possible as they fear the social consequences of poor performance (Sweet 1998).

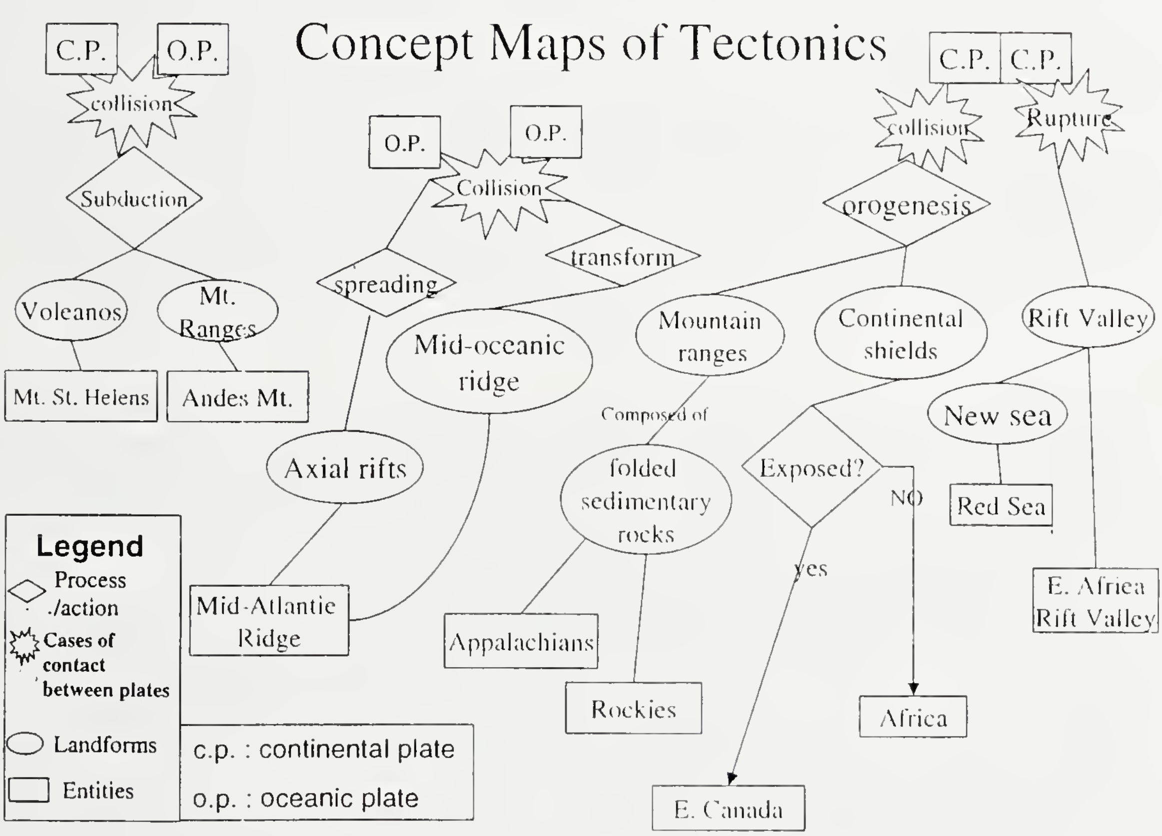
Concept Mapping

A concept map is a graphic representation constructed to show the relationships among concepts. Cognitive psychologists (Anderson 1985) postulate that learning is a process in which new knowledge is added to an existing knowledge web/network by creating associations to existing knowledge. A knowledge web consists of concept terms that are connected by annotated links to indicate the kind of relationships between concepts. For an example of concept mapping, please refer to Figure 1, which shows a concept map of tectonics produced as a course assignment by students. Pioneered by Novak (1977), concept mapping is applied to an education setting (Plotnick 1997) to a) generate and communicate complex ideas, b) design complex structure (Oughton & Reed 2000), such as in hypermedia/web presentations, c) aid learning (Plotnick 1997, Bolte 1999), and d) evaluate learning outcomes (Novak 1998). Educators, especially in science education (Plotnick 1997, Aidman & Egan 1998, Williams 1998, Bolte 1999, Kinchin 2000), have been using concept mapping to aid students in learning complex concepts. Most empirical studies (Williams 1998, Bolte 1999) support the idea that students learn better when they can visualize abstract entities.

Concept mapping can be used as an aid to help students digest content learned from lectures or readings. It is especially effective when there is a complex topic involving many interrelated concepts. For instance, one of this paper's authors used concept mapping to cover several textbook chapters regarding tectonics in a physical geography course. Tectonics is a theory with profound influences on the earth's landforms, and as a result dominates almost a half of the course content. Concepts and topics directly related to tectonics include earthquakes, volcanism, and orogenesis (mountain making process). The association can be extended to many other topics in the course (refer to Figure 1). It is difficult to develop lab experiments to demonstrate tectonic concepts due to the vast geologic time scale involved, and while fieldtrips to tectonic-affected sites may be of great educational value, they are often difficult and expensive to organize. Under such circumstances, a PBL module was developed to take advantage of the most economic and efficient learning source--the text. In the module, the importance of tectonics is first highlighted in a lecture that includes a video presentation showing tectonic landforms. Students are instructed to read the tectonic chapters after the initial lecture. When the class resumes, students work in small groups to construct concept maps of tectonics based on information presented in lecture, in video, and in the text. Much of the preparation for concept mapping was made on an individual basis and in off-class time. Class time is reserved for group work in order to reconcile differences in interpretation of the text and to

produce the map. This concept mapping activity not only covers a large ground in course content but also is more engaging than lecturing or a video presentation. Course evaluations show positive responses among most students, despite a few challenges that will be discussed later.

Novak and Symington (1982) point out that concept mapping acts as an interface between text and cognitive structures. As opposed to lectures or text in which information is presented in a linear sequence, concept maps organize information in a non-linear fashion. When students are assigned to construct a concept map based on lecture or reading content, they benefit from actively restructuring information from its linear sequence to a hierarchical structure. Concept mapping is a cognitively demanding task. It is this process through which students will try to make sense of the subject matter (Kinchin 2000).



Concept mapping may not be well received by students across the board. As expected, students who are accustomed to passive learning may not readily discover the benefit of this activity (Novak 1998, Kinchin 2000). The authors' experience also indicates that students' level of positive response to concept mapping is somewhat correlated with their academic performance and their attitude toward learning. On the other hand, instructors should not assume that students automatically possess skills required for concept mapping. It involves an entirely different set of skills to communicate via a visual/graphic medium. In addition, students typically feel intimidated and lost when first assigned to concept mapping. At times, they may also possess a viewpoint that is very different from the professor. For instructors, it is imperative to give students feedback during the construction of the concept map by being an active participant in the process.

In the tectonic module described above, students were given two class sessions to construct concept maps. At the end of the first session, the instructor sat down with each group to review their work, provide clarification, and to answer any questions. Assistance was also given during the session when groups became confused about some aspect of the tectonic process or failed to progress efficiently.

One of the greatest impediments to adopting concept mapping in a learning environment is assessment. Quantitative scoring on concept maps is neither straightforward nor problem-free (Kinchin 2000). It typically involves an *expert* map against which students maps are compared (Bolte 1999, Kinchin 2000). Some grading schemes require counting essential elements such propositions (concepts) and links; the others assess the magnitude of complexity and levels of hierarchy (Oughton & Reed 2000). Others evaluate student progress by comparing an initial concept map with a final, more complex, version of the product (Kinchin 2000). It does not help that all these strategies demand a good deal of grading time. Assessment of concept maps, therefore, remains an area of further research.

SUMMARY

PBL is a viable pedagogical approach despite its time-hungry nature. Course content demands in a PBL course may appear to be more severe when the course is situated in a non-PBL system where course sequence is a curricular concern. Nonetheless, with proper management and design, the problem of course content demands can be reduced to a minimum, and higher-order learning objectives can be achieved.

In this paper, we introduced two techniques that can be used for meeting course content demands in a PBL environment. Limited to the length of the paper, we had to omit discussion of several other methods. For example, assigning student groups a lecture to prepare can be an effective way to cover course content and to encourage cooperation. A carefully constructed series of problems can also expose students to most of a course's essential concepts. All of these techniques share some common elements. First, they are group activities with an individual component. In the case of the group quiz, students take the exam on an individual basis prior to the group exam. In concept mapping, student need to research into the topic individually before constructing the map. Second, these techniques create opportunities for group members to convene, brainstorm, and cooperate to accomplish a common goal. Higher order learning takes place during these activities even if

the task itself (such as the group quiz) involves only low-order comprehension and memorization. Third, these activities will not work without a proper structure to ensure individual accountability and cooperation among members.

This paper reflects part of the psychological journey the authors have experienced as we introduced PBL in our teaching. While we were pleased to observe a positive student response in PBL, we were often behind schedule! While experience seemed help us better manage class time, it gradually became clear that initial plans to incorporate PBL might have been too ambitious. We might have cared more about how much we teach, not how much students have learned. If PBL's premise of self-directed learning holds true, students should extend their learning to many occasions outside classroom. Course content demands should be deemed as a healthy and healthful sense of self-imposed responsibility, which forces us to make the best use of class time.

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A GEOGRAPHIC STUDY OF THE VEGETATION STRUCTURE OF BACHMAN'S SPARROW (*AIMOPHILA AESTIVALIS*) BREEDING HABITAT

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ABSTRACT

The vegetation structure of Bachman's Sparrow (*Aimophila aestivalis*) breeding habitat was studied in Arkansas, Alabama, Florida, South Carolina, and North Carolina. Bachman's Sparrows occupied areas with relatively low values (i.e., < 34%) in percent woody cover, tree density (203/ha) and percent forb cover, but with higher (i.e., > 58%) values in percent ground cover, percent grass cover, and percent litter cover. Vertical vegetation density was much higher under the 90 cm mark than above it. Univariate and multivariate statistics indicated significant differences in vegetation structure among the five study regions. Variables that showed little variation (e.g., percent litter cover, percent grass cover, litter depth, and vegetation density 0-90 cm) among the five regions may be more important in determining habitat suitability for Bachman's Sparrows, than variables that showed considerable variation (e.g., woody vegetation height, percent forb cover, and grass height).

INTRODUCTION

Species occupy a particular habitat for breeding because the habitat contains those environmental factors that allow a species to carry out its life history (Hilden 1965, James et al. 1984). One environmental factor that has been identified as being of considerable importance to avian species habitat occupancy is vegetation structure (MacArthur and MacArthur 1961, Hilden 1965, James 1971, Cody 1981, 1985). Birds are specifically adapted to a vegetation structure that meets their nesting, singing, and foraging requirements (Hilden 1965, Robinson and Holmes 1982, Cody 1985). For avian species that are declining and are of management concern, a thorough knowledge of the vegetation structure of the habitats that it occupies is critical (Martin 1992).

In most studies of habitat selection, the vegetation structure of occupied sites is compared to unoccupied sites and sampling is usually done in one general location within a species range (e.g., Haggerty 1986, 1998, Dunning and Watts 1990, Plentovich et al. 1998). Although this method may indicate the major features that determine occupancy, it does not necessarily indicate those features that may be the most critical for occupancy.

Another approach, and the one used in this study, is to compare the vegetation structure of occupied sites from a broad geographic perspective (James et al. 1984). If we assume that a species has similar foraging and nest-site selection behaviors throughout its range, then we can expect to see similarities in the vegetation structure of different localities, even though other variables (e.g., floristics, sere age, management practices) may be different. Similarities and differences in the vegetation structure from different localities may help identify structural features that are more or less critical for occupancy, respectively. Further, this approach may give a better understanding of the vegetation structure that may constrain the distribution of a species (James et al. 1984, Parrish 1995).

The Bachman's Sparrow is found primarily in open, grassy pine woods and early successional seres following clearcutting or pasture abandonment (Haggerty 1986, Dunning and Watts 1990). It nests and forages on the ground throughout its range (Dunning 1993). Although Bachman's Sparrow habitat studies have been done at different locations (Hardin et al. 1982, Wan A. Kadir 1987, Gobris 1992, Haggerty 1995, 1998, Plentovich et al. 1998), few comparative studies have been done (but see Dunning and Watts 1990).

Because declining Bachman's Sparrow populations may be due to strict habitat requirements and a loss of suitable habitat (Dunning and Watts 1990, 1991), research on its habitat use is of value. The objectives of this study were to quantify and compare the vegetation structure of Bachman's Sparrow breeding habitat from five geographic regions.

STUDY AREA AND METHODS

Vegetation samples of seven sites from Arkansas were made in June, July and August 1983-1985 in Hot Spring Co. and were part of a larger study (Haggerty 1986, 1998). Samples from Conecuh National Forest, Covington Co., Alabama (7 sites or tracts), Croatan National Forest, Carteret Co., North Carolina (4 sites), Ocala National Forest, Marion Co., Florida (5 sites), and Francis Marion National Forest, Berkeley Co., South Carolina (4 sites) were made between 8-20 July 1987. National forest sample sites were selected by playing a tape of a male song near sites that appeared to be suitable breeding habitat based on published descriptions (e.g., Brooks 1938, Meanley 1959, Mengel 1965, Wolf 1977, McKitrick 1979, Hardin et al. 1982) and personal experience. Once a male was located, sample circles (0.04 ha) were centered on the song perchs. In most cases, two samples were taken for each male. Twenty 0.04 ha sample circles were taken from each of the four national forests in the study and 65 were taken from the Hot Spring Co., Arkansas area. To insure an appropriate level of independence, data from sample circles for each site were pooled and the site was used as the sample unit in all statistical analyses.

Twelve variables were measured in a 0.04 ha circular plot using the methods of James and Shugart (1970) and Wiens (1973) (Table 1). Tree (dbh > 7.6 cm) density was determined by counting the number of live and dead trees within the sample plot. Vertical vegetation density was measured by counting the number of vegetation hits at two 90 cm intervals along a 180 cm rod held (6 mm diameter) vertically at ten equally spaced points along a transect that bisected the circle. Average woody, forb, and grass heights were calculated by measuring the height of the closest vegetation type at ten equally spaced points. Percent woody, forb, grass, and litter covers were estimated by noting if these

vegetation types came in contact with a vertically held rod that was placed at ten equally spaced points. Litter depth was measured within 2 cm of the base of the vertically held rod. Percent ground cover values were estimated by the presence or absence of standing vegetation at a cross-hair position in a sighting tube at 20 equally spaced points along two randomly oriented transects that bisected the plot.

Table 1. Descriptive statistics of 12 vegation variables and their correlation with two canonical variables from Bachman's Sparrow breeding habitat within five geographic regions (n=27).

Variable	**Mean(STD)**	**Min**	**Max**	**Can 1**	**Can 2**
Grass Height, cm	34.5(9.0)	18.7	59.8	-0.21	0.31
Forb Height, cm	34.9(11.4)	13.0	57.0	0.38	0.38
Woody Veg. Height, cm	68.4(37.9)	21.0	157.5	0.75***	0.23
Litter Depth, cm	1.1(0.8)	0.3	3.1	0.15	-0.56**
% Ground Cover	71.0(18.7)	35.0	95.0	0.38	-0.4
% Grass Cover	59.4(22.1)	20.0	97.5	0.37	-0.12
% Forb Cover	33.7(19.7)	2.5	67.8	0.79***	-0.16
% Woody Cover	31.1(17.9)	0.0	70.0	0.46*	0.03
% Litter Cover	76.8(16.7)	40.0	0.0	0.43*	0.12
Veg. Density 0 - 90 cm	5.3(3.3)	1.3	2.4	0.58**	-0.08
Veg. Density 91-180 cm	0.2(0.4)	0.0	2.0	0.46*	-0.44*
Tree Density/0.04 ha	8.1(6.1)	0.0	21.0	0.21	0.59**

***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$

One-way ANOVA's (PROC GLM), Duncan's multiple range test, and canonical discriminant function analysis (PROC CANDISC) were used to compare the vegetation structure between locations. Arcsine and logarithmic transformations were performed to normalize percentage and nonpercentage data, respectively (Zar 1974). Variables used in canonical discriminant analysis were approximately normal; therefore, it was assumed that the vector of variables associated with each sample point had an approximate multivariate normal distribution. Statistical significance was set at $P < 0.05$ for univariate tests. To help reduce the likelihood of type I error, a $P < 0.01$ was used for canonical discriminant analyses (Rextad et al. 1988). Pearson's product-moment correlations were used to assess the relationships among habitat variables and the canonical variable. All analyses were run using PC SAS (Version 6.01).

RESULTS

Univariate results of the five study regions combined indicate that Bachman's Sparrows occupied areas with relatively low mean values (< 34%) for percent woody cover, percent forb cover, and tree density, but higher values (> 58%) in percentages of ground cover, grass cover, and litter cover (Table 1). Average ground cover plant heights were less than a meter and the mean litter layer thickness was relatively thin. Vegetation vertical density was considerably higher under the 90 cm mark than above it (Table 1).

Univariate comparisons among regions showed that percent forb cover and woody vegetation height had the greatest amount of variation (Fig. 1A). These variables were significantly different among 6 and 8, of 10 possible regional comparisons, respectively (e.g., percent forb cover differed significantly between the Arkansas and Florida regions and between the Florida and South Carolina regions, Fig. 1A-1B). Grass height, forb height, tree density, and vegetation density 91-180 cm were significantly different among 4 of 10 possible regional comparisons (Fig. 1C-1F). Percent ground cover, percent woody cover, litter depth and vegetation density 0-90 cm showed less variation among the five regions, but were still significantly different (Fig. 1G-1J). Percent litter cover and percent grass cover were the only variables that did not significantly differ among the five regions (Fig. 1K-1L).

Specifically, univariate comparisons among the regions found that the sites in Arkansas and Florida, Arkansas and South Carolina, and Arkansas and North Carolina differed the most with seven variables being significantly different. Univariate comparisons showed that the vegetation structure of Alabama and South Carolina was the most similar (i.e., 2 variables differed). The other regional comparisons fell somewhere in between (Fig. 1).

Discriminant function analysis results indicated that the five regional centroids were significantly separated by the first (Wilk's Lambda = 0.0001, $F = 4.9$, $P < 0.0001$, eigenvalue = 17.0) and second (Wilk's Lambda = 0.01, $F = 3.4$, $P < 0.0001$, eigenvalues = 8.0) canonical variables. These two variables accounted for 58% and 28% of the variation among the regional tracts, respectively. The first canonical variable was significantly and positively correlated with percent forb cover, woody height, vegetation density 0 - 90 cm, and vegetation density 91 - 180 cm (Table 1). Regional points along the

first canonical variable indicate that Florida and North Carolina have low values for these variables, whereas South Carolina, Alabama and Arkansas have higher values (Fig. 2). The second canonical variable was positively correlated with tree density and negatively correlated with litter depth and vegetation density 91–180 cm (Table 1). Sites from South Carolina had higher tree density and lower litter depth values compared to Florida and Arkansas (Fig. 2).

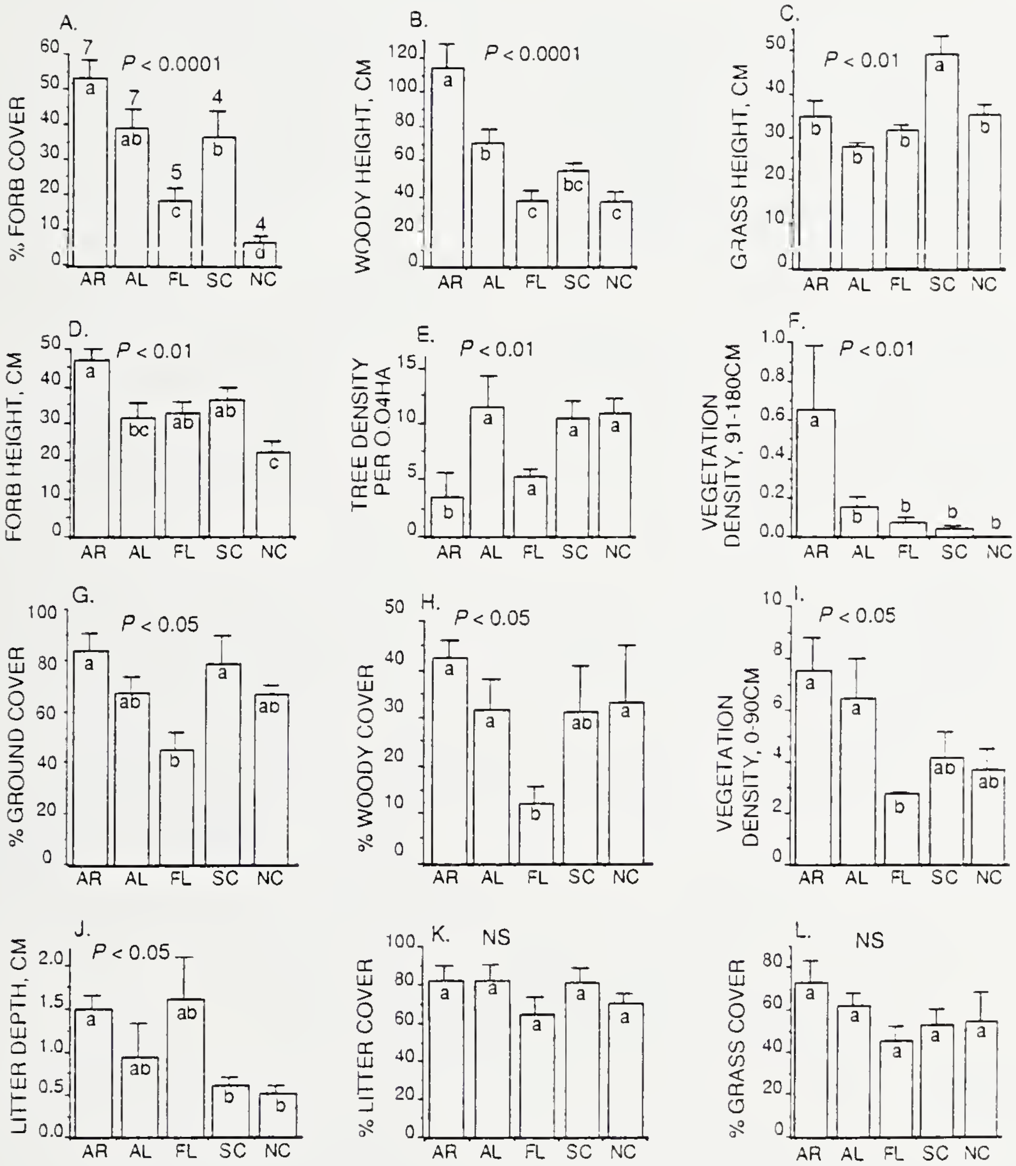
DISCUSSION

My results concur with others that have quantified the vegetation structure of Bachman's Sparrow breeding habitat (Hardin et al. 1982, Wan A. Kadir 1987, Dunning and Watts 1990, 1991, Plentovich et al. 1998). For example, studies in South Carolina (Dunning and Watts 1990) and Florida (Plentovich et al. 1998) found that Bachman's Sparrows also occupied sites that had more vegetation below the one meter point than above it and had relatively few trees and shrubs. Further, others have reported the dominance of grasses in the ground cover (Hardin et al. 1982, Wan A. Kadir 1987, Gobris 1992, Plentovich et al. 1998).

Some sampled tracts had zero or near zero values for percent forb cover, tree density, vegetation density 91-180 cm, and percent woody cover, indicating that Bachman's Sparrows may occupy areas where these structural features are absent or insignificant (Table 1). In South Carolina (Dunning and Watts 1990) and central Georgia (Gobris 1992), however, Bachman's Sparrows did not occupy open areas that had similar ground cover measurements to the occupied sites, but lacked scattered shrubs, trees, and other structures due to site preparation methods. Male and female Bachman's Sparrows regularly perch during song bouts and nest visits (Haggerty 1986, Haggerty 1992, pers. obs.) and occupied habitats may have to contain a vegetation component that can support the weight of a perched individual (Dunning and Watts 1990, Gobris 1992).

The preference throughout the species range for a ground cover composed primarily of grasses is not surprising considering Bachman's Sparrows foraging habits. Bachman's Sparrows forage relatively slowly and methodically, walking on the ground much like a foraging Ovenbird *(Seiurus aurocapillus)* (Allaire and Fisher 1975, pers. obs.). They feed on seeds and capture arthropods on the ground and on vegetation near the ground (Allaire and Fisher 1975, Haggerty 1992, pers. obs.). Short jumps at food items also occur and immobilized, captured prey are sometimes placed on the ground while the foraging adult strikes at a new food item (pers. obs.). This behavior allows for multiple food item delivery to growing nestlings (Haggerty 1992, 1994). A relatively dense, but patchy grass cover

Figure 1. Comparisons of the means (± 1 SE) of 12 vegetation variables from five regions within the breeding range of Bachman's Sparrow. Numbers above SE bars in (A) are number of tracts sampled from each region. Significant differences among regions were examined using one-way ANOVA's. Regional bars that do not share similar letters are significantly different using Duncan's multiple range test.


A.
P < 0.0001
% FORB COVER
B.
P < 0.0001
WOODY HEIGHT, CM
C.
P < 0.01
GRASS HEIGHT, CM
D.
P < 0.01
FORB HEIGHT, CM
E.
P < 0.01
TREE DENSITY PER 0.04HA
F.
P < 0.01
VEGETATION DENSITY, 91-180CM
G.
P < 0.05
% GROUND COVER
H.
P < 0.05
% WOODY COVER
I.
P < 0.05
VEGETATION DENSITY, 0-90CM
J.
P < 0.05
LITTER DEPTH, CM
K.
NS
% LITTER COVER
L.
NS
% GRASS COVER
AR AL FL SC NC

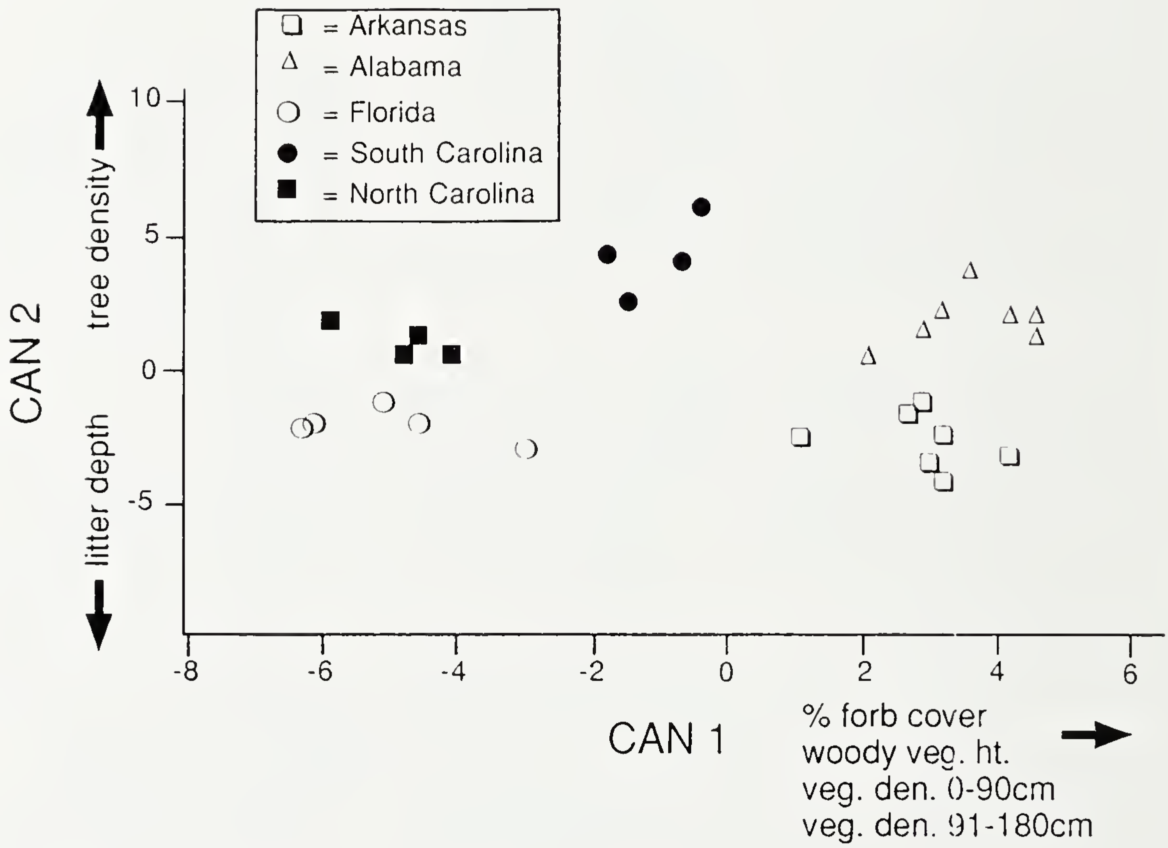


Figure 2. The location of sampled tracts from five state regions along two canonical discriminant function axes. Variables significantly correlated with canonical axes are shown.

offers a plentiful substrate for prey near the ground, yet permits Bachman's Sparrows good visibility and maneuverability for capturing and manipulating food. High percentages of forb and woody vegetation cover may provide less surface area for arthropods at ground level. Trees and shrubs shade out grasses and therefore reduce foraging sites for arthropods. Further, the base of grass clumps are the preferred nest site for Bachman's Sparrows (Haggerty 1988, 1995). In Arkansas, 50 of 71 (70%) nests were placed at the base of *Andropogon* spp. grass clumps (Haggerty 1988).

The low variation in percent litter cover among regions also indicates that structural features at ground level may be important for occupancy. Litter may provide habitat for potential prey, yet too much litter may impede movement and reduce the foraging success of this obligate ground-feeding sparrow. An increase in ground level debris following a hurricane was suspected for the failure of previously occupied sites in being selected by Bachman's Sparrows (Dunning and Watts 1991). Haggerty (1998) found that unoccupied sites had significantly more litter than occupied sites providing additional evidence that Bachman's Sparrows may be sensitive to litter cover.

In conclusion, although all the regions sampled are in the same physiographic region (i.e., Coastal Plain Province; Brouillet and Whetstone 1993), six of the 12 variables measured were significantly different among regions at the 0.01 level, four at the 0.05 level, and only two were not significant. Further, three canonical discriminant functions significantly separated the five study regions. This variation may be due to numerous factors, such as differences in population preferences, floristics, management practices, and sere age. The dissimilarity in vegetation structure among regions, however, may also indicate that Bachman's Sparrows are more tolerant of a wider range of variation for some variables (e.g., percent forb cover, woody vegetation height, grass height, forb height, tree density and vegetation density 91-180 cm) than for others (e.g., percent ground cover, percent woody cover, vegetation density 0-90 cm, litter depth, percent litter cover, and percent grass cover). These findings may have important management implications. Variables that showed the greatest amount of variation among regions may be less important in determining if a habitat is suitable for occupancy. Likewise, variables that showed little variation among locations (e.g., percent grass cover, percent litter cover, litter depth) may be structural features that Bachman's Sparrow are more sensitive to and should be more closely managed.

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EFFECTS OF EXOGENOUS JUVENILE HORMONE ON VITELLOGENESIS IN THE CRICKET, *ACHETA DOMESTICUS* (L.)

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ABSTRACT

Vitellogenesis, yolk formation in developing oocytes, consists of two processes in insects: vitellogenin (Vg) production by the fat body and Vg uptake by terminal follicles within ovarioles of vitellogenic ovaries. The role of juvenile hormone (JH) in regulating these processes was examined in the European house cricket, *Acheta domesticus* (L.). Decapitation was used to remove the corpora allata, the source of JH in intact animals. Uptake of a vital dye, trypan blue, by terminal follicles and total ovarian dry weight were used to assess the vitellogenic activity of the ovary, and SDS-polyacrylamide gel electrophoresis was employed to detect hemolymph Vg. Both components of vitellogenesis were abolished by decapitation, and this was shown to be due to the absence of a factor from the head rather than to starvation. The vitellogenesis deficiencies in decapitated animals were corrected by a single injection of 10 μg of JH I into the abdomen at the time of decapitation. The results indicate that JH has a prominent role in regulating vitellogenesis in this orthopteran, but they do not eliminate the possibility that other endocrine factors from the cerebral and/or retrocerebral neuroendocrine systems may also have regulatory functions in vitellogenesis.

INTRODUCTION

The corpora allata (CA), paired-sphere shaped organs of the retrocerebral neuroendocrine complex, are the glandular source of juvenile hormone (JH) in insects. In most nondipteran species, JH regulates vitellogenesis (Engelmann, 1983). The action of JH in yolk formation occurs at two levels: first, on the fat body to induce transcription of the gene(s) for vitellogenin (Vg), the blood borne precursor of egg yolk protein (Engelmann, 1984; Engelmann *et al.*, 1987; Glinka and Wyatt, 1996), and second, on the follicle itself to

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support uptake of Vg from the hemolymph (Telfer *et al.*, 1982; Bradley, 1983; Sevala *et al.*, 1995).

The effect of allatectomy upon ovarian development in *Gryllus (Acheta) domesticus* was examined by Belyaeva in 1967. He found that in animals allatectomized within two days after ecdysis to the adult, oocyte development was arrested at the beginning of yolk deposition. On the other hand, females containing 4-6 implanted CA began oviposition earlier than intact control animals and the total number of eggs oviposited during the first 10 days of adult life was greater for animals receiving implants than for control animals. The effect of reimplantation of CA into allatectomized hosts was not reported.

Although much effort has been directed toward understanding the hormonal control of egg maturation in other orthoperans, most notably *Locusta migratoria* (Glinka *et al.*, 1995; Glinka and Wyatt, 1996; Sevala *et al.*, 1995; Wyatt *et al.*, 1996), Belyaeva's work is the only study to date directly concerned with the endocrine control of ovarian growth in *A. domesticus*. The only other related studies in the cricket are those of Renucci and Strambi (1983) reporting hemolymph JH titers during ovarian development and Benford and Bradley (1986) showing that exogenously administered JH can induce vitellogenin (Vg) synthesis in young adult females decapitated soon after ecdysis to the adult.

In this article we report *in vivo* effects of exogenously administered JHs and JH-mimics (JHMs) upon some aspects of vitellogenesis, the stage at which oogenesis in Belyaeva's allatectomized animals became arrested.

MATERIALS AND METHODS

Experimental animals

Batches of 1000 mixed males and females of *Acheta domesticus* were purchased from Fluker's Cricket Farm, Inc. (Baton Rouge, LA). Stock populations were maintained at room temperature as previously described (Bradley and Edwards, 1978). Experimental animals were removed from the stock population midway through their last (9th) larval instar, isolated in 150 mm diameter x 25 mm high plastic Petri dishes, and either starved or supplied with pulverized food pellets (Little Friskies, Carnation Co.) and water in cotton-stopped vials *ad libitum*. The dishes were kept in a Sherer controlled environment chamber at 26-27°C on a 12L-12D photoperiod at 70% RH, and a folded, plain white 7.5 x 12.5 index card was placed in each arena to provide protected areas for molting. Animals were checked 2-3 times daily for ecdysis to the adult which usually occurred 6-8 days after the nymphs were isolated from the stock population. The time of ecdysis (2 hours) was estimated for each imago by its cuticular color and degree of wing inflation as described in Table 1.

Allatectomy was accomplished within 12 hours of ecdysis to the adult, prior to the onset of yolk deposition, by neck-ligation with dental floss followed immediately by decapitation. The ovaries were then examined for vitellogenic follicles on day 5. Control animals were food- and H_20-starved for the same period of time.

Before dissections animals were cold-immobilized within a glass beaker by a 5-10 minute exposure to crushed ice beneath the beaker. Alternatively, animals were sometimes

stored for 3-5 hours at 4°C before dissection. This treatment also results in complete immobilization.

TABLE 1

DETERMINATION OF TIME OF ECDYSIS TO THE ADULT IN *ACHETA DOMESTICUS* AT 26-27°C

Appearance of Animal	Time Elapsed from Ecdysis
Pure white except for black eyes. Wings ruffled, not fully inflated	0-15 minutes
Body pure white. Wings straight and smooth	15-60 minutes
Body white except for light tan thorax	1-2 hours
Light gray of abdomen visible beneath wings	2-3 hours
Overall appearance light gray	3-4 hours
Overall appearance slate-gray	4-5 hours
Overall appearance slate brown	5-6 hours
Overall appearance brown	more than 6 hours

Administration of hormone mimics and exogenous JH I

Juvenile hormone mimics (JHMs) ZR512 (ethyl 3,7,11-tri-methyldodeca-2,4 dienoate) and ZR512 [isopropyl (2E,4E)-11-methoxy-3,7,11-tri methyl-2,4-dodecadienoate] were dissolved in light mineral oil (Fisher, Saybolt viscosity 125/135) to give a final concentration of 20 $\mu g/\mu l$ for each JHM. Animals were injected dorsolaterally with 5 μl of this solution through an intersegmental membrane behind the 4th abdominal segment on the right-hand side of the animal. A 50 μl Hamilton syringe equipped with a punch-button microliter dispenser and a 4mm long 30G needle were used for the injections. Concentrated JHMs and stock solutions of JHMs in mineral oil were stored at -20°C. ZR515 and ZR512 were gifts from Lynn M. Riddiford, University of Washingtion. Both compounds are obtainable from Zoecon Corporation, Sagami Chemical Company. Juvenile hormone I in which the *trans, trans, cis* isomer accounted for either 75% or 95% the material was purchased from Eco-Control, Inc. Animals were injected with 10 ug of JH I in 5 ul of mineral oil as described above for the JHMs.

Bioassay for JH activity

The biological activity of the *t,t,c*-JH I compound from Eco-Control, Inc. was tested using the *black mutant* larval pigmentation assay in the tobacco hornworm, *Manduca sexta*, according to Fain and Riddiford (1975). Mutant *M. sexta* larvae were kindly provided by Dr. Lynn Riddiford, Zoology Department, University of Washington.

Ovarian maturation assays

The incidence of unchorionated, vitellogenic follicles and fully mature, chorionated follicles was determined by stereomicroscopic examination of freshly dissected ovarian tissue using side illumination against a black background. Ovaries were placed in 0.14M NaCl in a shallow watchglass at ambient temperatures, and the ovarioles were teased apart using watchmaker's forceps. Most ovulated, chorionated oocytes became dispersed from the remaining ovarian tissue and had a glassy surface texture under these conditions. Unchorionated, vitellogenic follicles were opaque white or blue (in cases where they had taken up exogenously administered trypan blue) and were easily distinguishable from the transparent previtellogenic follicles anterior to them within the ovarioles. Dye injected animals were administered 50-100 μl of a 1% solution of the vital dye, trypan blue, in 0.14M NaCl through an abdominal, intersegmental membrane 8-12 hours before examination of the ovaries.

Ovarian dry weight was determined by first carefully removing visible, adhering fat body tissue from the ovaries using forceps and microscissors while they were viewed in 0.14M NaCl under a steriomicroscope. Each ovary was then rinsed quickly in distilled water and transferred to a small plastic, predried, pre-weighed weigh tray. Trays and ovaries were placed in shallow Pyrex glass dishes and dried at 60°C until a constant weight was obtained. Ovarian dry weight was calculated as the difference between the weight of the pre-dried tray and the same tray containing the dried ovary.

Polyacrylamide gel electrophoresis

Hemolymph and egg yolk protein samples were prepared for denaturing polyacrylamide gel electrophoresis (SDS-PAGE) as previously described (Bradley *et al.*, 1987). SDS-PAGE was performed according to Laemmli (1970) in mini-gels containing 7.5% acrylamide and using a Bio-Rad (Model Mini-PROTEAN II) apparatus. Polypeptides in the gels were fixed and visualized by staining with 0.1% Coomassie brilliant blue G250 in 10% acetic acid and 50% methanol. The gels were destained in 7% acetic acid and photographed over a light box with Technical Panatomic Film (Kodak). Markers for molecular weights were obtained from Sigma Chemical Co. (Product MW-SDS-200).

Light microscopy

Fixation of ovarian tissue was begun *in situ* by flushing the opened abdomen of live animals several times with 0.5% glutaraldehyde and 2% paraformaldehyde in Millonig's Phosphate buffer, pH 7.2. The ovaries were then removed and fixed 2-3 hours at room temperature in the same fixative, post-fixed in 2% osmium tetroxide in Millonig's phosphate buffer, pH 7.2, for one hour at room temperature, and embedded in Epon. One micron thick sections were transferred to glass microscope slides and stained over an alcohol flame with Richardson's stain (Azure II and methylene blue, 1:1 (Richardson *et al.*, 1960). Micrographs were produced by conventional bright field microscopy using Kodak Ectachrome film.

RESULTS

Assessing the vitelllogenic state of A. domesticus

Events constituting insect vitellogenesis include the biosynthesis of vitellogenin (Vg) by the fat body, Vg secretion into the hemolymph, and uptake of Vg by vitellogenic follicles. Generally only the terminal follicle within an ovariole is vitellogenic, there being a distinct demarcation between the previtellarium and the vitellarium of the ovariole. Vitellogenic follicles can be identified visually by their uptake of trypan blue injected into the abdominal cavity. The sharp transition between previtellogenic follicles and the vitellogenic follicle in an ovariole is clearly seen in Figure 1a where no sign of dye uptake is detectable in the smaller, transparent, subterminal follicle. By contrast the ooplasm in the larger, terminal vitellogenic follicle is opaque due to the uptake of the dye. A surface view of the same vitellogenic follicle obtained by flattening the follicle beneath a coverslip shows a honeycomb-like pattern in the follicular epithelium surrounding the oocyte (Fig. 1c). We interpret the dark outlines of follicle cells to be due to the presence of trypan blue in spaces between the follicle cells. To gain further insight into the cellular basis for the intense, specific staining of terminal vitellogenic follicles by trypan blue, bright field microscopy of sectioned, Epon embedded tissue was used to compare the structure of the follicular epithelium and peripheral ooplasm in previtellogenic follicles to that in vitellogenic follicles. Follicles in the previtellarium were enveloped by a squamous epithelium in which the cells are tightly abutted against each other (Fig. 1b). Each squamous epithelial cell possessed a single, ovoid nucleus, and the ooplasm was relatively homogeneous, showing no evidence of yolk spheres. By contrast, the follicular epithelium of vitellogenic follicles was columnar and possessed distinct spaces between the cells (Fig. 1d). The nuclei in these cells were bipartite, and the ooplasm was filled with large lipid droplets and smaller, membrane-bound yolk spheres. Numerous, vesicles were visible in the cortical ooplasm in close proximity to the apical ends of the follicle cells (Fig. 1d).

That trypan blue injection is an efficacious way to survey entire ovaries for the incidence of vitellogenic follicles is shown in Figure 2 (top) where several ovarioles have been teased away from an ovary removed from an injected animal and then viewed with a dissecting microscope. The specificity of dye uptake by vitellogenic follicles is apparent, there being no evidence of dye inside the small, clear previtellogenic follicles lying anterior to the stained, terminal follicles. The dye was also clearly absent from fully grown, chorionated oocytes (Fig. 2, top). Interestingly, occasional, opaque white follicles were present in ovaries of dye-injected animals. These we presume to be early vitellogenic follicles

Figure 1. Transition from previtellogenic to vitellogenic oocyte growth. a) stereomicroscopy of live ovariole from trypan blue injected female showing previtellogenic follicle (left) and vitellogenic follicle (right), b) bright field microscopy of Epon embedded, sectioned previtellogenic follicle with squamous epithelium (arrow) and germinal vesicle (GV), c) bright field microscopy of surface of live, vitellogenic follicle from female injected with trypan blue, d) bright field microscopy of peripheral region of sectioned, vitellogenic follicle; L, lipid droplet; P, protein containing yolk spheres; arrow, small endocytic vesicles in cortical ooplasm near apical side of columnar epithelium. Scale bars: 1a = 50 μm; 1b-1d = 10 μm.

Figure 1

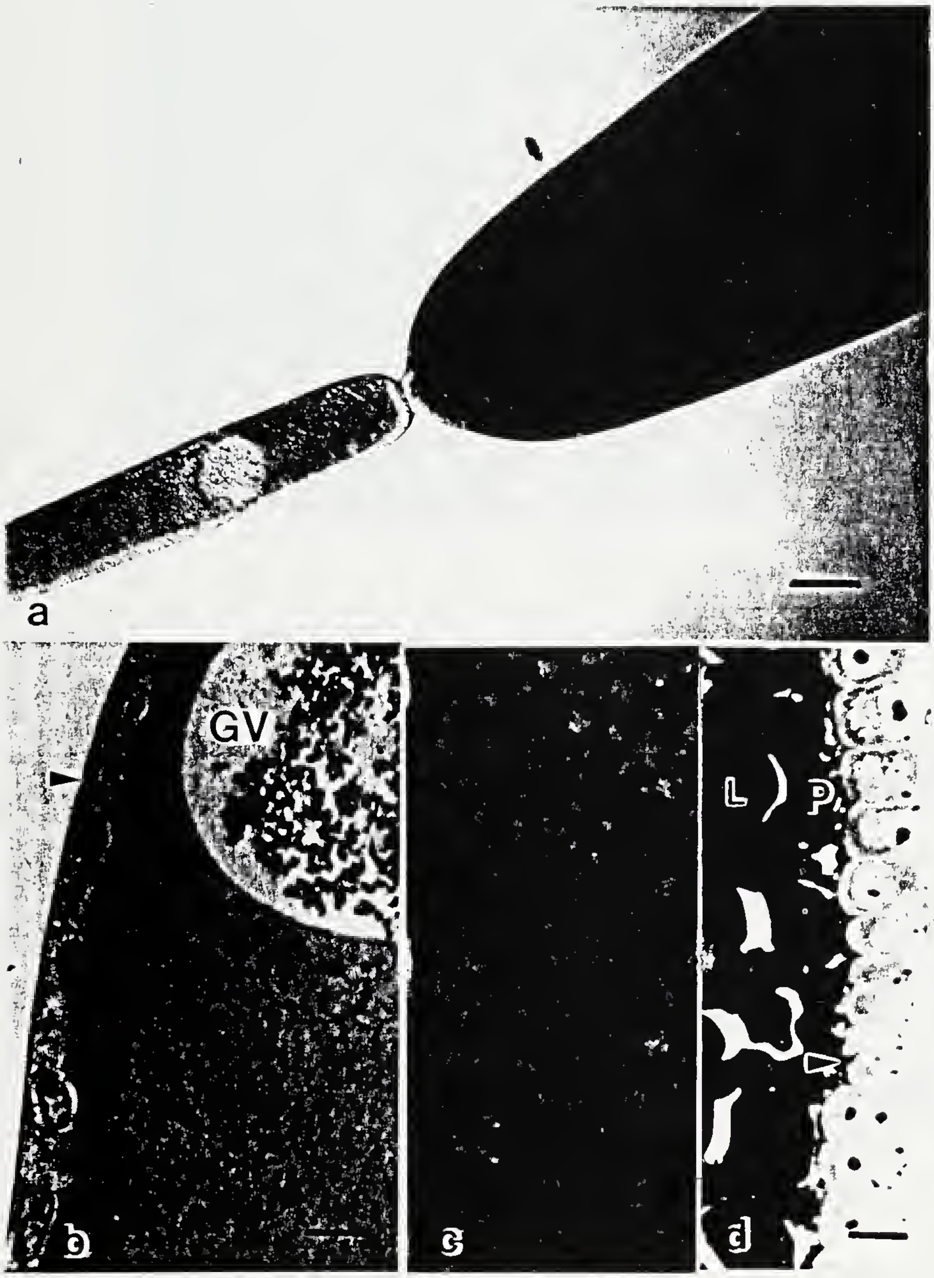
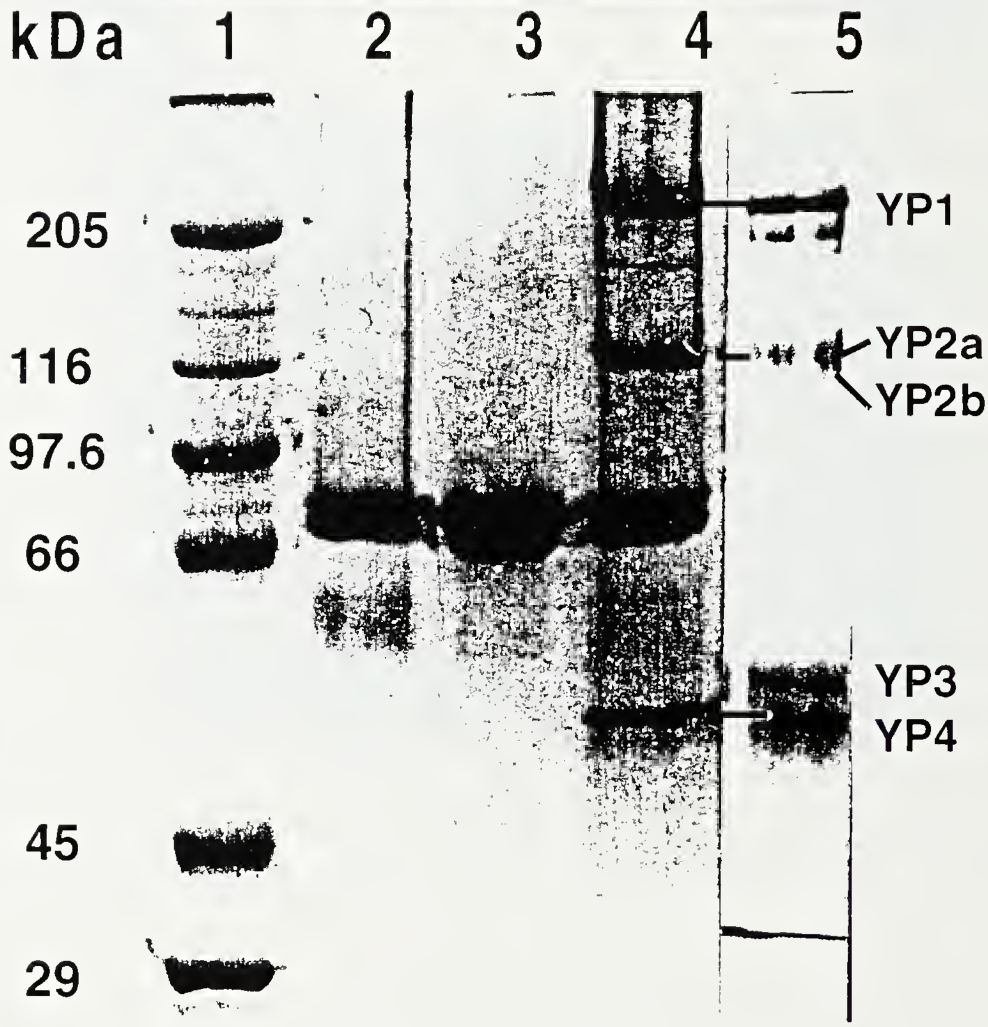


Figure 2



in which dye uptake did not occur. Taken together, the observations described above gave us confidence in using the total number of ovarian follicles per individual taking up trypan blue as an index of vitellogenic activity in the ovary for the experiments that follow.

Since it is possible that Vg synthesis and Vg uptake are regulated independently, it was desirable to have an assay for Vg that reflects the biosynthetic/secretory activity of the fat body. For this purpose we chose to exam the hemolymph from living animals for the presence of Vg. In Figure 2 (bottom) are shown the results of separating hemolymph polypeptides from male and female animals by SDS-PAGE. Vitellogenin is identifiable as adult female-specific polypeptides which comigrate with their counterparts in an extract of egg yolk protein. Three such polypeptides, YP1, YP2a, and YP4, with molecular masses circa 50-200 kDa were readily identifiable in the hemolymph of adult females (Fig. 2, bottom). None of these were detectable in the hemolymph of mature males or larval stage females.

Vitellogenesis in starved animals, neck-ligated animals, and neck-ligated animals receiving replacement therapy with JHMs

Allatectomy in *A. domesticus* can be accomplished by decapitation due to the location of the CA in the anterior region of the neck near the base of the head capsule. To determine whether removal of the CA affects subsequent vitellogenesis in *A. domesticus*, adult females were decapitated prior to the onset of yolk deposition and examined by stereomicroscopy for opaque white vitellogenic follicles on day 5 (Table 2, Experiment 1). Control animals were food- and H_20-starved for the same period of time. No vitellogenic eggs were observed in decapitated females. That this effect is not solely nutritional is indicated by the fact that 66% of the starved control animals produced vitellogenic follicles during the same period. Failure of decapitated animals to produce vitellogenic follicles was not corrected by supplying the animal with 100 μg of the ZR512 JHM at the time of ligation. Starved animals injected with paraffin oil produced as many vitellogenic eggs as the starved controls, indicating that the paraffin oil used as a carrier for the JHM did not inhibit vitellogenesis.

In Experiment 2 (Table 2), the number of vitellogenic follicles per animal was scored on day 6 by counting the number of oocytes which had accumulated visually detectable levels of trypan blue after its injection into the abdominal cavity. By this assay it was determined that decapitated, paraffin oil-injected animals can produce a few vitellogenic follicles. There was not a significant difference between the number of dyed follicles present in decapitated control animals and the number present in animals that had been administered either the ZR512 or ZR515 JHM at the time of decapitation. The mean number of vitellogenic follicles produced by starved, control animals was significantly higher than that produced by decapitated controls receiving paraffin oil alone.

Figure 2. Assays for vitellogenesis in *A. domesticus*. **Top**, ovarioles from ovary of trypan blue injected, adult female. Scale bar = 1 mm. **Below**, SDS-PAGE of hemolymph and yolk polypeptides; lane 1, molecular mass markers; 2, adult male hemolymph; 3, last larval instar hemolymph; 4, adult female hemolymph; 5, egg yolk extract. YP, yolk polypeptide; kDa, kilodaltons.

Experiment 3 (Table 2) was performed to determine whether a factor from the head must be continuously available in order for vitellogenesis to continue once it has started. Adult, virgin females 9-10 days past ecdysis and therefore midway into their reproductive cycle were either starved or ligated and decapitated. Eighteen hours later they were injected with a trypan blue solution, and 5 hours after that the ovaries were scored for both the number of opaque, white vitellogenic oocytes and the number of oocytes having taken up the dye. The incidence of actively endocytic (blue) oocytes as a percentage of the total number of follicles having initiated vitellogenesis (white plus blue) is reported for each group in Table 2. Among the decapitated animals, only about half of all follicles in the yolk deposition stage of oogenesis actually sequestered dye; whereas, virtually all similar staged follicles in the starved control animals were endocytic.

Effect of replacement therapy by exogenous JH I upon oocyte growth in neck-ligated crickets

The absence of any observed effect by either of the two Zoecon compounds upon the incidence of vitellogenic follicles does not indicate that Vg uptake in the cricket is JH-independent since it is possible that these JHMs are either inactive in crickets or are rapidly metabolized to inactive forms. The effect of the occurring hormone, JH I, upon vitellogenic growth of the ovary was therefore assessed. First, the hormone was tested for its biological activity using the black mutant larval pigmentation bioassay in *M. sexta*. A linear dose-response curve was obtained within the range .01 - 1 μg JH I/larva (Fig. 3). Next, in order to determine whether total ovarian dry weight can be used as a measure of the vitellogenic growth of the ovary, the relationship between the dry mass of the ovary and the length of the longest, terminal, vitellogenic follicle was determined. A linear relationship between the two parameters was observed until fully grown (2.0 - 2.5 mm long) follicles began appearing in the ovary (Fig. 4). Thereafter, increased ovary mass, due to yolk uptake by the subterminal follicles just anterior in the ovarioles to fully grown chorionated oocytes, is not reflected in an increase in terminal oocyte length since these have already attained their maximum length. Since the relationship between the parameters is linear until fully grown oocytes are present, it was concluded that ovary dry mass is a reliable index of the level of vitellogenic development that has been attained by an ovary that is accumulating yolk.

Table 2 Effect of decapitation and injection of JH-mimics (JHM) upon initiation and maintenance of vitellogenesis. In experiments 1 and 2 animals were neck-ligated and then decapitated within 12 hours after adult ecdysis. Starvation was also begun in control animals at 12 hours after adult ecdysis. Animals were given injections of JHM or mineral oil alone immediately after decapitation or at the time of initiation of starvation. The presence of vitellogenic eggs by day 5 (Expt. 1) or the number of vitellogenic eggs per animal by day 6 (Expt. 2) was recorded. In experiment 2 vitellogenic eggs were identified by their uptake of trypan blue. In experiment 3 animals were starved or decapitated 9-10 days after ecdysis and injected with trypan blue 18 hours later. The percentage of vitellogenic eggs active in dye uptake was then recorded.

TABLE 2

Vitellogenesis in Decapitated, Starved, and JH-mimic Treated Animals

Experiment 1	N	% Animals with Vitellogenic Eggs
Decapitated	10	0
Decapitated + 100 mg ZR512	9	0
Starved control	15	66
Starved control + 5 ml mineral oil	7	71

Experiment 2		No.Dyed Eggs / Animal
Decapitated + 5 ml mineral oil	9	20.0 ± 6.7
Decapitated +100 mg ZR512	10	21.8 ± 5.0
Decapitated +100 mg ZR513	8	14.3 ± 4.1
Starved Control + 5 ml mineral oil	8	37.2 ± 6.6

Experiment 3		% of Yolky Eggs Actively Vitellogenic
Starved	6	96.6 ± 2.1
Decapitated	5	52.0 ± 20.1

Juvenile Hormone

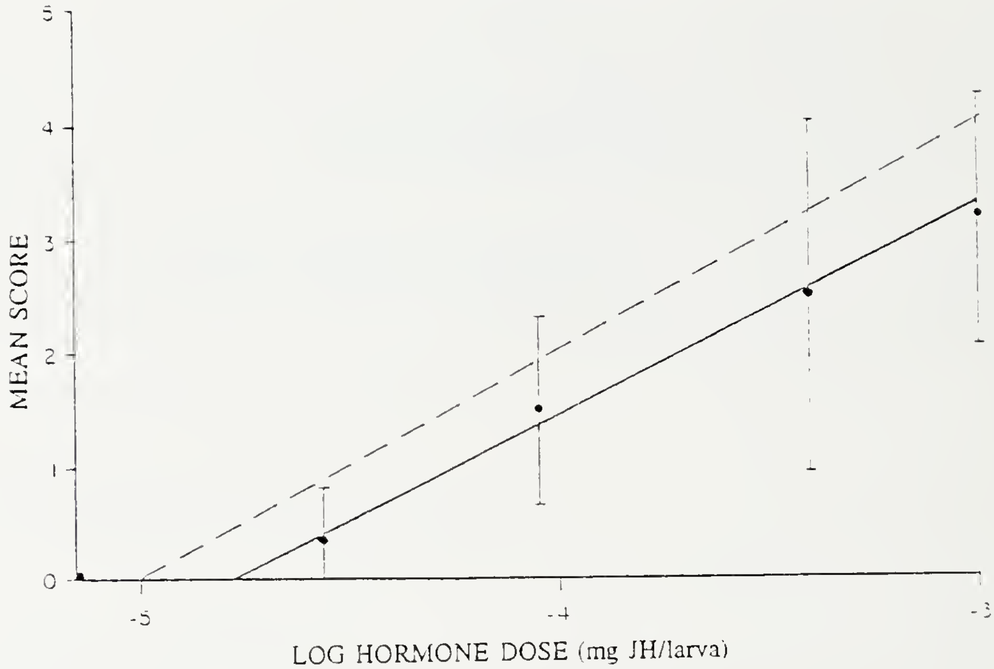


Figure 3. Dose response curve for juvenile hormone activity of 95% pure *trans, trans, cis* JH I in the *black mutant* larval pigmentation assay in *M. sexta*. Twenty larvae were used for each point which represents the standard deviation of the mean.

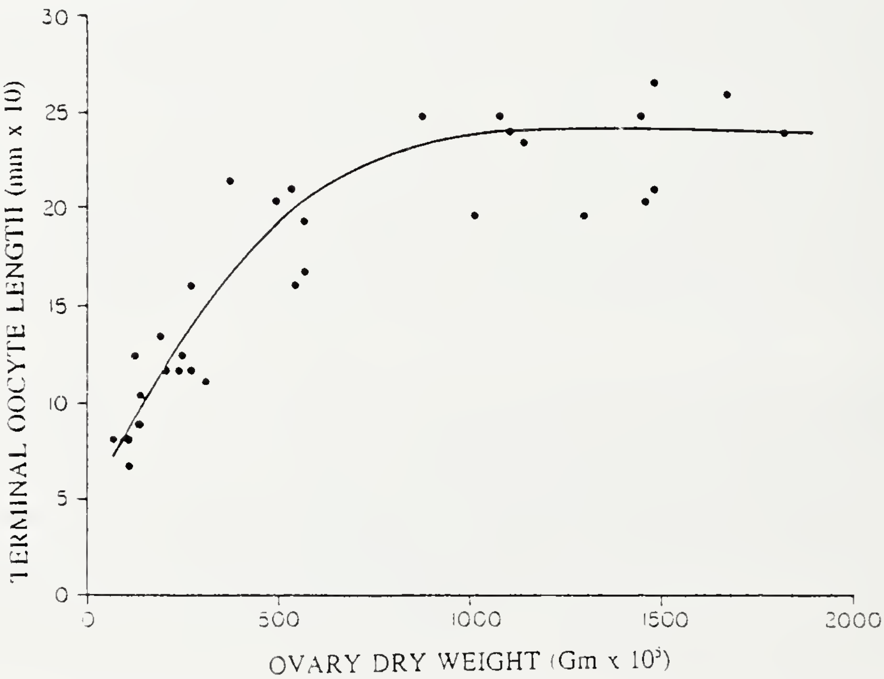


Figure 4. Relationship between length of terminal, vitellogenic, follicle and total dry weight of the ovary in young adult females.

of the ovary in young adult females.

Experiments were done to determine whether supplying exogenous JH I soon after adult ecdysis enhances the rate of vitellogenesis as measured by ovarian dry weight attained by 4- 5 days following ecdysis. Since the first fully grown eggs do not appear until days 4 - -5 (Bradley and Edwards, 1978), the rate of increase in ovarian dry weight should be directly related to terminal follicle growth during this early phase of the reproductive cycle. Two experiments were performed. In the first, the JH I used contained 75% the *trans, trans, cis* isomer whereas the second experiment utilized JH I containing 95% the *trans, trans, cis* isomer. The results for both experiments are reported in Table 3. In experiment 1 10 μg of JH I in 5 μl of paraffin oil were injected abdominally within 19 hours after ecdysis. In experiment 2 the same protocol was followed except that administration of the hormone was at 48 hours after ecdysis to the adult. Control animals received only 5 ul of paraffin oil. Treatment with both forms of exogenous JH increased the rate of vitellogenic ovarian development (Table 3), the compound containing 95% *t,t,c*-isomer having the most pronounced effect even though the period of exposure to the hormone was shorter for this compound.

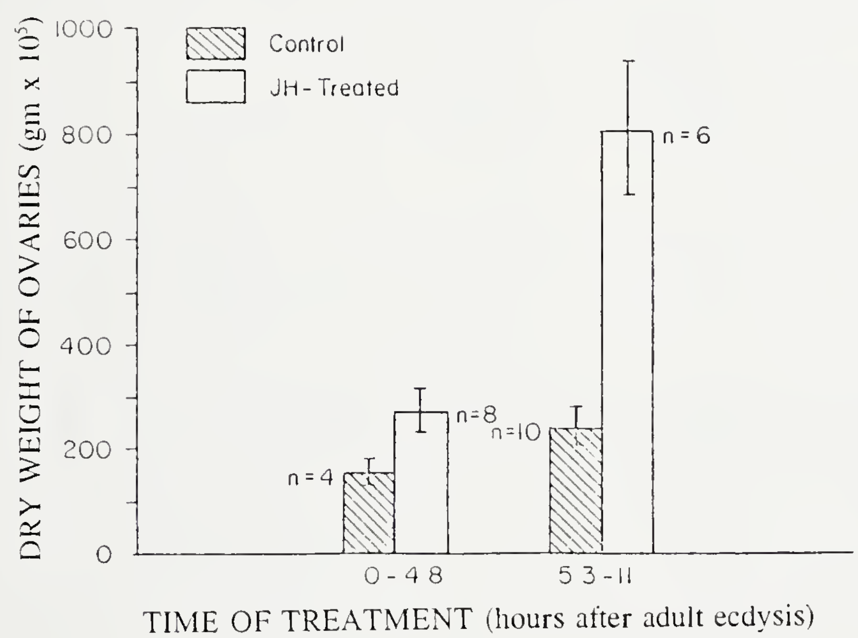


Figure 5. Effect of time of JH I treatment upon subsequent ovarian development. Data points for the control and JH-injected animals of Table 3, Experiment 1 have been separated into two groups: (1) those representing animals injected within 5 hours after ecdysis and (2) those representing animals injected 5-11 hours after ecdysis. The histograms represent the mean ($\pm$ standard error) ovary dry weight attained by the experimental and control animals 4- 4.5 days after ecdysis.

The time after ecdysis at which the 75% *t,t,c* JH isomer was injected had an affect on the mass attained by the ovary during the period after hormone administration. Enhancement of ovarian growth by the exogenous JH became greater the later the hormone was administered (Fig. 5.) Ovarian growth in control animals receiving the carrier alone was unaffected by the time of treatment.

To determine whether stimulation of ovarian growth was affected by the site of injection, the mass of the right and left ovaries of the animals injected with the 95% *t,t,c* JH isomer (Table 3, Experiment 2) were measured separately. Each animal was injected on the right-hand side of the abdomen. Although the mean dry weights of the right and left ovaries were not significantly different (right ovary, 363.8 ± 49.4 X 10^{-5}gm; left ovary, 326.4 ±46.5 X 10^{-5}gm), it is interesting that in 9 of the 12 animals, the dry weight of the right ovary was greater than that of the left ovary.

TABLE 3

Effect of JH I Upon Ovarian Growth

Experiment 1	N	Adult Age at Time of Treatment (hours)	Adult Age at Sacrifice (days)	Ovary dry weight (gm x 10^5) ±std. error
Control (5 ml paraffin oil)	15	1-19	4-4.5	205.9 ± 24.8
Experimental (10 μg JH I 75% *t, t, c*)	15	1-19	4-4.5	528.4 ± 91.5
Experiment 2				
Control (untreated)	12	N/A	5	446.9 ± 56.3
Control (5 ml paraffin oil)	8	48	5	393.6 ± 45.1
Experimental (10 μg JH I 95% *t, t, c*)	12	48	5	733.6 ± 98.5

Effect of injection of JH I upon ovarian development in normal, virgin females by 4-5 days following adult ecdysis. Animals were isolated from a stock population midway through their last larval instar and kept in individual Petri dishes at 26-28°C.

Exogenous JH and appearance of yolk protein in decapitated females

The above results suggest a role for JH in Vg uptake. To examine the role of JH in the prerequisite Vg synthesis/secretion, an experiment was done to determine whether decapitation prevents the appearance of yolk proteins in the hemolymph, and if so, whether the deficiency can be corrected by supplying exogenous JH I. In normal females, Vg polypeptides were detectable in Coomassie blue-stained gels during the third day following ecdysis to the adult (Fig. 6). Animals were therefore decapitated a day earlier, and blood samples were collected from each animal immediately prior to decapitation and again during the third day of adult life (Table 4, Samples I and II). Analysis of the blood for YP2a, the Vg polypeptide most easily detected by SDS-PAGE, showed that no control animals lacking Vg at the time of decapitation had detectable Vg in their blood a day later, whereas 60% of the JH-treated females and all of the intact, starved control animals had produced detectable amounts of Vg. Normal appearing yolky, terminal follicles were present in ovarioles of all starved animals and in one of the JH-injected decapitated animals in which Vg was also present.

DISCUSSION

Decapitation to remove the CA, the glandular source of JH, and subsequent JH replacement therapy provided evidence that several aspects of vitellogenesis are regulated by JH in the cricket, *A. domesticus*. We acknowledge that our experiments do not rule out the possibility that other hormones and neuroendocrine centers might be involved in regulating vitellogenesis in the intact animal. In addition to the CA, decapitation removes the median neurosecretory cells of the pars intercerebralis (PIC), the corpora cardiaca which serve as paired neurohemal organs for the products of the cerebral neurosecretory cells, intrinsic neurosecretory cells of the corpora cardiaca, and the nervus CA II which contain neurosecretory material. In fact, an endocrine interaction between the ovary and the brain of *A. domesticus* is suggested by earlier work showing that ovariectomy results in a decrease in the amount of paraldehyde fuchsin (PAF) positive material in the PIC and decreased levels of several PAF positive polypeptides in the brain and corpora cardiaca (Bradley and Simpson, 1981). Moreover, electrocautery of the PIC of *A. domesticus* results in decreased egg production but does not abolish the formation of some fully grown, yolk filled eggs (Bradley, 1976). Since a few neurosecretory cells remained undestroyed after electrocautery in these experiments, the possibility remains that a brain neurohormone is an absolute requirement for normal egg maturation in *A. domesticus* as is the case for certain other insects including *Sarcophaga bullata* (Wilkins, 1968), *Aedes taeniorhyncus* (Lea, 1964), and *Locusta migratoria* (Girardie, 1966). That JH synthesis by the CA is controlled by the brain and/or subesophageal ganglion is well established for many insects, and both neuronal and non-

TABLE 4

Appearance of Vitellogenin in Decapitated, JH I-treated Animals

Treatment	Adult Age, Sample I (hours)	YP 2a Detected? I	II	Adult Age, Sample II (hours)
Decapitated,	46	-	-	80
Mineral oil	46	-	-	80
-injected	46	+	+	80
	51	+	+	75
Decapitated,	51	-	+	75
JH-injected	51	-	+	75
	51	-	+	75
	51	-	-	75
	51	-	-	75
Starved	42	-	+	80
	48	-	+	94
	51	-	+	74
	53	-	+	74

Effect of exogenous JH upon appearance of Vg polypeptide, YP 2a, in hemolymph of decapitated females. Two days after adult ecdysis animals were either decapitated, decapitated and injected with 10 ug of JH I in 5 ul of mineral oil, or food and H20-starved.

A hemolymph sample (2.6 ul) was collected at the time of initiation of the above treatment (Sample I). One to 2 days later a second hemolymph sample was collected (Sample II). The blood samples were electrophoresed in 6% acrylamide SDS-gels and the presence (+) or absence (-) of YP 2a scored for each animal at the beginning and end of the given treatment. Ages of each animal at the time Samples I and II were collected are indicated.

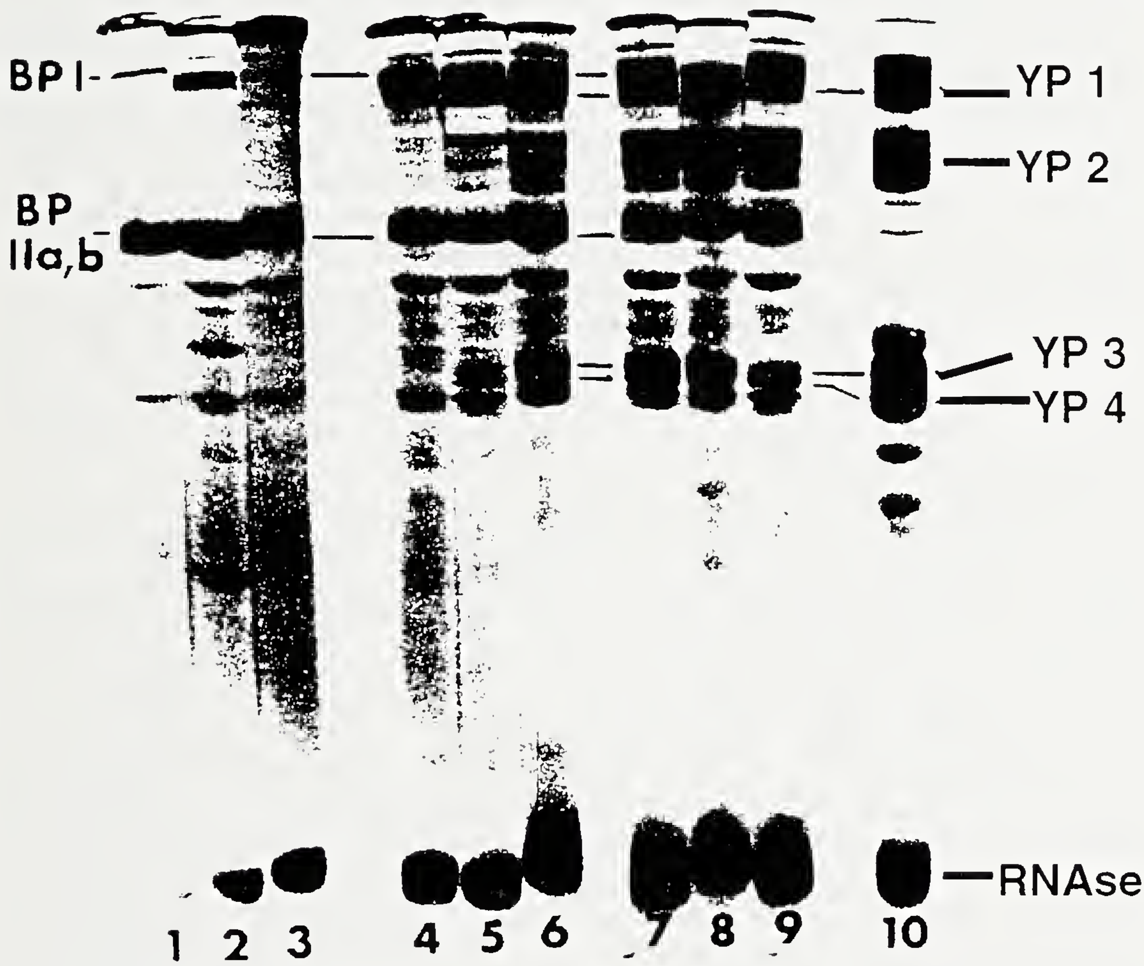


Figure 6. Time course for appearance of Vg polypeptides (YPs) in hemolymph of a representative, young adult female. Polypeptides were separated by SDS-PAGE in tube gels and stained with Coomassie brilliant blue. Hemolymph samples (2.6 μl) were collected at the indicated times after ecdysis: 1.5 hrs (Gel 1), 20.5 hrs (2), 26.5 hrs (3), 43 hrs (4), 66 hrs (5), 77.5 hrs (6), 3 da 19.5 hrs (7), 4 da 3 hrs (8), 4 da 23 hrs (9). BP, non-sex-specific blood polypetides; RNAse, ribonuclease as low molecular mass marker.

neuronal pathways for CA regulation have received intense study during the past decade (Gilbert *et al*, 2000).

Notwithstanding these caveats to the interpretation of our decapitation experiments, the fact that JH I replacement in headless animals supported Vg production and uptake suggests that JH is the final endocrine signal in any putative endocrine pathway that includes JH and ultimately results in the induction of vitellogenic activity in the fat body and developing follicles. The ability of JH I to induce the appearance of Vg in the hemolymph of decapitated females (Table 4; Bradley and Benford, 1986) strongly indicates that JH is responsible for induction of Vg synthesis in *A. domesticus*. Our experiments also indicate that JH enhances the rate of uptake Vg uptake by vitellogenic follicles (Tables 2 and 3). Whether this enhancement is due to JH action upon the follicle itself as has been demonstrated in the blood sucking bug, *Rhodnius prolixus* (Davey, 1981; Sevala *et al.*, 1995) or to an increased titer of Vg in the hemolymph is not known. Kunz and Petzelt (1970) proposed that yolk protein synthesis is the rate limiting step for vitellogenesis in *A. domesticus* reproduction; however, in the roach, *Nauphoeta cinerea*, Vg synthesis was induced by small doses of exogenous JH, while stimulation of oocyte growth required higher doses (Lanzrein, 1979). This suggests that Vg synthesis and uptake are regulated independently in this species. In *A. domesticus*, the increased growth rate of the ovary on the JH-injected side of the animal could be due either to a localized enhancement of Vg synthesis by the fat body resulting in a higher concentration of Vg in the vicinity of that ovary or by an enhancement of Vg uptake by the oocytes of that ovary.

Injection of the JH-mimics, ZR512 or ZR515 (Table 2 Experiments 1 and 2) into decapitated animals did not correct the vitellogenesis deficiency in these animals. This suggests either that these compounds are not active in *A. domesticus* or that they are rapidly metabolized to biologically inactive compounds. Production of some vitellogenic follicles by decapitated females receiving mineral oil (Experiment 2, Table 2) suggests that a low level of JH activity exists in the mineral oil itself.

It is well established that in *A. domesticus* and other insects, Vg in the hemolymph gains access to the oocyte surface during vitellogenesis via spaces that develop between adjacent cells in the follicular epithelium (Telfer et al., 1982; Dennis and Bradley, 1989; Bradley and Estridge, 1997). It then enters the ooplasm via receptor-mediated endocytosis (Raikhel and Dhadialla, 1992). We exploited these aspects of the cell biology of vitellogenesis to develop a trypan blue bioassay for the action of JH on vitellogenic follicle growth in *A. domesticus*. We suggest that the assay is based on the endocytic uptake of the dye by the oolemma of vitellogenic oocytes. Although we have not demonstrated that trypan blue becomes incorporated into membrane bound yolk spheres as does Vg, it is reasonable to assume that this is the case since only terminal follicles in each ovariole sequester the dye and since the dye colocalizes with Vg in the spaces between follicle cells (Fig. 1; Bradley and Estridge, 1997). Whether trypan blue competes for Vg during the endocytic process or is taken up along with Vg, perhaps by being bound to it, is not known.

That the nutritional state influences egg development was shown by experiments in which animals were starved for varying periods of time. Although the appearance of Vg polypeptides in the blood and yolk formation and/or trypan blue uptake were not prevented

by short-term starvation (1-4 days), starvation over longer periods of time (5-6,days) resulted in cessation of yolk deposition and resorption of vitellogenic follicles (data not shown). We conclude that activation of the endocrine pathway(s) required for vitellogenesis does not require a signal resulting from food intake after ecdysis to the adult; however, continued support of normal ovarian development does require nutrition, perhaps to maintain Vg synthesis or alternatively, to sustain CA activity. Future experiments in which exogenous JH is administered to starved animals may be able to distinguish between these two possibilities.

That a factor from the head is required for maintenance of vitellogenesis is shown by Experiment 3, Table 2, in which decapitation midway through the reproductive cycle resulted in a 50% reduction in the percentage of yolky oocytes that remain endocytically active 18 hours later. In this experiment, endocytic activity was detected by the trypan blue assay which showed terminal follicles to be either opaque white, lacking any detectable dye, or very darkly stained, indistinguishable from those of intact crickets shown in Figures 1a and 2. This suggests that the endocytic activity in any given terminal follicle in these decapitated animals was either normal or completely lacking.

Whether this decreased incidence of endocytically active follicles is due to a decreased titer of Vg in the hemolymph or to a direct effect upon the follicle itself is not known. In either case, interesting questions arise as to differential sensitivities of follicles within a single female to the nutritional and/or hormonal mileau of the animal. If a decreased titer of Vg leaves some follicles active and others inactive, there is an implied threshold titer of Vg for each follicle, below which no uptake occurs. Discovery of how such thresholds for individual follicles might be set and detected would provide hitherto unknown information about the physiology of vitellogenesis. Alternatively, if it is a decrease in the titer of JH or another endocrine factor that leaves some follicles active and others inactive, there arises the equally interesting problem of how gonadotropin levels might produce a dichotomous population of terminal follicles.

Our use of JH I in the above experiments deserves an explanation since JH I is not a major JH in the Orthoptera as it is in higher insect orders such as the Lepidoptera (Gilbert et al., 2000). In fact, the CA of *A. domesticus* synthesize and secrete JH III *in vitro* (Strambi, 1981). Nevertheless, an earlier study showed JH I to be ten times more active than JH III in a Vg induction bioassay in *A. domesticus* (Benford and Bradley, 1986). That JH I is more active than the naturally occurring hormone in *A. domesticus* may be because it has a longer half-life in the hemolymph than JH III, perhaps reflecting the greater polarity of JH III that may render it more susceptible to degradation (Gilbert, 2000). It is also possible that the specificity of JH esterases in *A. domesticus* is toward the endogenous JH III. In *N. cinerea* the juvenilizing activity of exogenous JH I, was ten-fold higher than that of exogenous JH III even though the elimination rate of the former was much higher than that for JH III (Lanzrein, 1979). This suggests that their stability in the hemolymph is not always the most important factor in determining the relative activities of different JHs for a species.

In summary, decapitation of *A. domesticus* soon after adult ecdysis mimicked the effect of allatectomy obtained by Belyaeva (1967), and exogenous JH I is able to induce and maintain vitellogenesis in decapitated, adult female *A. domesticus*. The simple assays we have described for assessing endocytic activity by vitellogenic follicles and production of

hemolymph Vg should prove useful in future work designed to assess the mode of action of JH on vitellogenesis and the possible roles of other endocrine factors in the regulation of vitellogenesis in this orthopteran.

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